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Ecological interactions between abalone, urchins and benthic

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(PhD) Quantative Marine Science

"Ecological interactions between abalone, urchins, and benthic habitat in a temperate reef ecosystem: implications for ecosystems based management"

By

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School of Zoology & Tasmanian Aquaculture and Fisheries Institute

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Declarations

Statement of Originality

This thesis contains no material that has been accepted for a degree or diploma by the University or any other institutions. To the best of my knowledge this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text.

Date: 20.01.10

Elisabeth Marijke Anne Saskia Strain

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Statement of co-author contributions

Chapters 2-7 of the thesis have been prepared as a series of manuscripts for publication in peer reviewed journals. Please see the title of each chapter for further details. In all cases the design and implementation of the research, data analysis, interpretation and preparation of the manuscript was the responsibility of the candidate in consultation with supervisors and other contributors. The contributions of each author are outlined below.

Chapter 2: Prof. Craig Johnson contributed conceptual and practical knowledge about the ecological interactions between urchins and abalone. Dr. Russell Thomson contributed statistical expertise to undertake the Marklov chain modelling.

Chapter 3: Prof. Craig Johnson contributed conceptual and practical knowledge about the ecological interactions between urchins and abalone.

Chapter 4: Prof. Craig Johnson contributed conceptual and practical knowledge about urchin and abalone ecology and the dynamics of temperate rocky reefs.

Chapter 5: Prof. Craig Johnson contributed conceptual and practical knowledge about abalone ecology and the dynamics of temperate reef ecosystems

Chapter 6: Prof. Craig Johnson contributed conceptual and practical knowledge about abalone ecology and the dynamics of temperate reef ecosystems

Chapter 7: Prof. Craig Johnson contributed conceptual and practical knowledge about the interactions between abalone and other components of temperate reef ecosystems.

ABSTRACT

The Tasmanian blacklip abalone (*Haliotis rubra*) fishery supplies ~25% of the world market and, with a value of ~AUD$120 M p.a., is the State's most valuable fishery. Fishing pressure is intense and management has been based on 'single-species' methods. However, with clear recognition that the fishery depends on the ecosystem that supports it, there is growing demand for a broader ecosystems based management approach (EBM). This thesis examined the ecological interactions between *H. rubra* and the invasive urchin (*Centrostephanus rodgersii*), and whether fishing of *H. rubra* leads to a shift in the benthic community structure to a habitat configuration that becomes less favourable for abalone.

Previous surveys demonstrated a negative relationship between densities of *C. rodgersii* and *H. rubra*. We used manipulative experiments to examine the effect of competition on behaviour, movement, growth, and survival. Removals of *H. rubra* had no detectable effect on *C. rodgersii*, so there is no evidence that fishing of abalone contributed to the urchin invasion success. In contrast, introducing *C. rodgersii* to intact algal beds caused *H. rubra* to flee and seek shelter in cryptic microhabitats, and reduced their growth and survival rates, all of which would negatively impact on the abalone fishery. *H. rubra* only ventured into small *C. rodgersii* barrens after urchins were removed and these areas revegetated. This suggests that lack food and/or loss of biogenic habitat structure explain the absence of abalone on barrens. The combined research suggests that EBM of *C. rodgersii* to optimise the *H. rubra* fishery requires complete removal of urchins and regrowth of barrens.

Surveys at a range of spatial scales, depths and locations demonstrated a positive relationship between cover of encrusting red algae (ERA) and densities of *H. rubra*, and a negative relationship between densities of abalone and cover of filamentous algae, sessile invertebrates and the sediment matrix. Removal of *H. rubra*, to simulate heavy fishing, resulted in overgrowth of ERA by sessile invertebrates and a matrix of filamentous algae and sediment. Emergent *H. rubra* actively avoided areas overgrown by the matrix, which may negatively impact the fishery. Because *H. rubra* ostensibly prefer an open bottom dominated by ERA, these changes create a positive feedback loop. Above some threshold, more fishing is likely to render a greater proportion of the benthos unsuitable for abalone. Since *H.*

rubra depletion can cause a shift to habitats poorly conducive to abalone, EBM should consider the effects of fishing on benthic habitat structure.

CHAPTER 1: GENERAL INTRODUCTION

Globally, many commercial fisheries are in decline (Jackson et al. 2001, Pauly et al. 2002, Myers & Worm 2003, Scheffer et al. 2005). Major anthropogenic stressors include global climate change (Walther et al. 2002), invasive species (Carlton & Geller 1993), fishing (Jackson et al. 2003, Myers & Worm 2003), pollution, nutrients, (Islam & Tanaka 2003), and habitat loss (Lotze et al. 2006). These stressors can result in declines in species abundances, and alter the ecological interactions between species, and their environment (Scheffer & Carpenter 2003, Folke et al. 2004, Hughes et al. 2005). With the increasing risk of multiple anthropogenic stresses there is an unprecedented risk of a dramatic shift in species composition, known as catastrophic, phase or regime shifts, which are often long lasting and difficult to reverse (Scheffer & Carpenter 2003, Folke et al. 2004, Hughes et al. 2005). Hence, scientists and managers have an urgent need to understand the ecological interactions between species and their environment that support or undermine the systems resilience to human impacts (Hughes et al. 2005, Mangel & Levin 2005).

Regime shifts in temperate rocky reef ecosystem

Major perturbations can cause shifts between alternative stable species communities (Scheffer et al. 2001, Steneck et al. 2002, Hughes et al. 2005). Regime shifts in temperate rocky reef systems, with severe economic and social consequences include the shift between kelp beds and urchin barrens (Chapman & Johnson 1990, Tegner & Dayton 2000), and the irreversible collapse of many coastal and oceanic fisheries (Jackson et al. 2001, Meyers & Worm 2003, Ward & Myers 2005). These alternative species communities can persist indefinitely and are maintained by internal reinforcing processes and stabilized by negative feedback loops (Beisner et al. 2003, Collie et al. 2004, Hughes et al. 2005, Scheffer et al. 2001). Although many striking regime shifts have been observed in temperate rocky reef systems, mechanistic explanations for the dynamics of the transition and the processes that maintain their stability remain scarce, particularly in spatially complex systems (Scheffer & Carpenter 2003, Schroder et al. 2005).

Ecosystems based management of abalone fisheries

Abalone are herbivorous macro-invertebrates, that are primarily located in the intertidal and subtidal areas of temperate rocky reef ecosystems (Shepherd 1973, Shepherd et al. 2001). Abalone fisheries have traditionally focused on single-species based management strategies (Shepherd et al. 2001, Jenkins 2004). However, with growing awareness that abalone both affect and depend on the dynamics of the rocky reef ecosystems that support them, there is impetus to develop and apply ecosystem based management (EBM) strategies to abalone fisheries to complement the established practises based on single species (Jenkins 2004, Shepherd et al. 2001). This approach requires a good understanding of the interactions between abalone and other components of the temperate rocky reef ecosystem, to manage the systems resilience to human impacts.

The case study: Blacklip abalone

Blacklip abalone (*Haliotis rubra*) is a large and abundant macro-invertebrate, found across a wide range of habitats and wave exposures in southeast Australia (Shepherd 1973). In Tasmania, this species supplies ~25% of the world market and, with a value of ~AUD$120 M p.a., is the State's most valuable fishery. (Jenkins 2004). EBM of this fishery requires a good understanding of the ecological interactions between *H. rubra* and other species and their environment. Here we investigate the ecological interactions between *H. rubra* and the invasive long spined urchin (*Centrostephanus rodgersii*) and the effects of fishing on benthic habitat structure.

Interactions between *H. rubra* and *C. rodgersii*

Driven by increased poleward penetration of the East Australian Current (Ridgway 2007) the urchin *C. rodgersii* has undergone a southerly range expansion from New South Wales and was first recorded in mainland Tasmanian waters in 1978 (Edgar 1997, Johnson et al. 2005, Ling et al. 2009). In intact algal beds, *C. rodgersii* and *H. rubra* co-occur in similar habitat, and share predators and some overlap in diet. This urchin is well known for its ability to overgraze algal beds, resulting in a catastrophic shift to an alternative stable barrens habitat (Johnson et al. 2005, Ling 2008). *C. rodgersii* barrens are becoming more widespread along the east coast of Tasmania and do not support viable fisheries of *H. rubra* (Johnson et al. 2005). Whereas much of the research on the impacts of *C. rodgersii* on *H. rubra* densities has focused on barrens habitat, the nature of interactions

between these 2 herbivores in intact algal beds, before any commencement of destructive urchin grazing, is not well understood (Andrew & Underwood 1992, Andrew et al. 1998, Johnson et al. 2005). Assessing the effects of interspecific competition between *C. rodgersii* and *H. rubra* in intact algal beds is important to understand the mechanism behind the successful establishment of this urchin and the eventual exclusion of the abalone.

The range expansion of *C. rodgersii* into Tasmania is predicted to have major negative impacts on local biodiversity, biogenic habitat and the interactions between native species (Edgar et al. 2004, Johnson et al. 2005, Ling 2008). In New South Wales, large scale removals of *C. rodgersii* resulted in overgrowth of extensive barrens by filamentous and foliose algae and sessile invertebrates, with concomitant increases in the densities of *H. rubra* (Andrew et al. 1998). These results suggest that *C. rodgersii* has a negative impact on populations of *H. rubra,* although the mechanisms remain unclear. Understanding the direct and indirect impacts of *C. rodgersii* on *H. rubra* is important for developing EBM strategies.

Effects of intensive fishing *H. rubra* on benthic habitat structure

Intensive fishing of marine consumers can result in a catastrophic shift between alternative stable states (Jackson et al. 2003, Myers & Worm 2003). Anecdotal evidence from abalone fishers and researchers alike suggests that sustained depletion of *H. rubra* can lead to a shift in benthic structure from habitat characterised by encrusting red algae (ERA), that is non-calcareous red algae (NERA) and non geniculate coralline algae (NCA), to a community dominated by sessile invertebrates, filamentous algae, and a matrix of sediment interspersed with filamentous algae. If *H. rubra* plays an important role in maintaining community dominated by ERA to the exclusion of the filamentous algae, sessile invertebrates and sediment matrix, then a substantial reduction in abalone biomass as a result of fishing may lead to a change in both ecosystem structure and function (Shepherd et al. 2001, Jenkins 2004).

Any activities that reduce the cover of ERA could also have important implications for the long-term persistence of *H. rubra* populations. Abalone larvae preferentially metamorphose after contact with ERA, and juvenile abalone feed on these algae associated bacteria and diatoms until they reach approximately 15 mm in length (Shepherd 1973, Morse & Morse 1984, Daume et al. 1999). Shell pigmentation from phycoerythrin and other

phycobiliprotiens obtained through feeding on ERA also aids camouflage, and ostensibly providing protection from predators during this critical early life history phase (Shepherd & Turner 1985, Kitting 1997). The relationship between *H. rubra* and ERA could be characterized as a positive feedback loop; encrusting red algae promote settlement, growth and survivorship of abalone while abalone grazing promotes ERA. Thus, intensive fishing of *H, rubra* could result in a regime shift to an alternative stable state which then becomes unsuitable for abalone populations.

Thesis structure

This thesis examines the ecological interactions between abalone and urchins and benthic habitat. The thesis begins by exploring interactions between *H. rubra* and *C. rodgersii* in intact algal beds, and barrens habitat. We examine whether fishing of *H. rubra* results in a shift in benthic habitat structure which then becomes unsuitable for abalone populations. We then review the processes leading to, and implications of regime shifts, for EBM of abalone fisheries. The thesis has been developed as a series of manuscripts for publication, and thus each data chapter represents a stand-alone manuscript. Consequently, some repetitions in the introductions of several chapters was unavoidable.

Chapter 2, 3 & 4 examines the nature and effects of interactions between *H. rubra* and *C. rodgersii*. **Chapter 2** assesses the effects and relative magnitude of intra- and interspecific competition on abalone and urchin behaviour, movement patterns, and local abundances in open plots, in intact algal beds. **Chapter 3** quantifies the effects and relative magnitude of intra- and interspecific competition of food on abalone and urchin body condition, reproduction, and survival in experimental enclosures in intact algal beds. **Chapter 4** investigates the direct and indirect impacts of *C. rodgersii* on the distribution and abundances of adult and juvenile *H. rubra* and *H. erythrogramma* in barrens using a removal experiment.

Chapter 5 & 6 examines whether fishing of *H. rubra* leads to a shift in benthic habitat structure which then becomes unsuitable for abalone. **Chapter 5** describes the relationship between the abiotic and biotic habitat characteristics and the abundances and mean size of adult *H. rubra* at a range of spatial scales, depths and locations. In **Chapter 6**, we used a suite of experimental manipulations to test whether intensive fishing of blacklip abalone (*Haliotis rubra*) leads to overgrowth of non-calcareous encrusting

red algae (*Peyssonnelia* spp. and *Hildenbrandia* spp., NERA) and non-geniculate coralline algae (NCA) by filamentous and foliose algae and sessile invertebrates and accumulated sediment and experimental transplants to determine whether any shift in habitat characteristics subsequently affects the distribution and abundance of adult abalone.

In **Chapter 7** we review our results in the context of published research to provide an overview of the direct and indirect interactions between abalone and other components of the temperate rocky reef ecosystem, and their implications for EBM strategies.

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CHAPTER 2: EFFECTS OF CLIMATE INDUCED RANGE EXPANDING URCHIN ON COMMERCIALLY FISHED ABALONE

ABSTRACT

Global climate change has resulted in the southerly range expansion of the barrens-forming urchin (*Centrostephanus rodgersii*) into Tasmania, Australia. Surveys on the southeast coast of Australia have shown a negative relationship between densities of *C. rodgersii* and *H. rubra* at several spatial scales, suggesting negative interactions. We used an experimental framework to examine the effects of interspecific competition on *C. rodgersii* and intra- and interspecific competition on *H. rubra,* behaviour, movement and local abundances, in intact algal beds. Manipulations of *H. rubra* densities had no detectable effects on *C. rodgersii* behavioural transitions, movement patterns or resightability. In contrast, additions of *C. rodgersii* or extra *H. rubra* to plots, resulted in fewer abalone remaining exposed and an increase in the proportion of sheltering and mobile abalone and the mean net distance moved by abalone relative to controls. Additions of *C. rodgersii* to plots also lead to a decline in the resightability of *H. rubra*, relative to controls. There were no detectable effects of the translocation procedures on the resightability of *C. rodgersii* or the tagging procedures on the resightability of *H. rubra.* There were also no detectable differences in the numbers of predators (*Jasus edwardsii* and fishes) between treatments. Our results suggest that there are asymmetrical competitive interactions between *C. rodgersii* and *H. rubra.* The introduction of *C. rodgersii* to intact algal beds causes *H. rubra* to flee and seek shelter in cryptic microhabitat which will potentially negatively impact on their accessibility and productivity for the abalone fishery, while the presence of the abalone has no detectable effect on the urchin. This framework could be used to understand impacts of other climate induced range expanding species on other native species.

Keywords: climate change, range extension, competition, *Centrostephanus rodgersii, Haliotis rubra*

INTRODUCTION

Global climate change is leading to the redistribution of many non-indigenous marine species with the potential to modify biogenic habitat (Ling 2008), alter the interactions between native species (Smith 2005). and result in declines in local biodiversity (Firth et al. 2009). Competitive interactions between non-indigenous and native species can influence invasion success (Baltz & Moyle 1993) and negatively impact on native species (Byers 2000 a b, Bohn & Amundsen 2001, Jensen et al. 2002). The paucity of information about competitive interactions between many non-indigenous and native species limits our understanding any potential impacts of range expansion on marine ecosystems, and hinders efforts to prioritise management responses (Carlton 1992).

Driven by increased poleward penetration of the East Australian Current (Ridgway 2007) the long spined urchin (*Centrostephanus rodgersii*) has undergone a southerly range expansion from New South Wales and was first recorded in mainland Tasmanian waters in 1978 (Edgar 1997, Johnson et al. 2005, Ling et al. 2009). This urchin is well known for its ability to overgraze productive and diverse algal beds, and maintain bare rock barrens habitat (Fletcher 1987, Johnson et al. 2005, Ling 2008). *C. rodgersii* barrens are becoming more widespread along the east coast of Tasmania, and do not support viable fisheries of blacklip abalone *Haliotis rubra* (Andrew & Underwood 1992, Andrew et al. 1998, Johnson et al. 2005). Whereas much of the research on the impacts of *C. rodgersii* on *H. rubra* has focused on barrens habitat the nature of interactions between these 2 herbivores before any commencement of the destructive grazing is not well understood. Assessing the effects of interspecific interactions between *C, rodgersii* and *H. rubra* in intact algal beds could be important for understanding the factors leading to the successful establishment of the urchin and the eventual exclusion of abalone.

In intact algal beds, *C. rodgersii* and *H. rubra* are the largest macro-invertebrate herbivores and since they share similar predators and some overlap in habitat and dietary components, it has been widely speculated that they compete for resources (Shepherd 1973, Andrew & Underwood 1992, Andrew et al. 1998, Johnson et al. 2005). Evidence for interspecific competition between urchins and abalone is often given as negative correlations between their abundances, and has been reported from south east Australia (Shepherd 1973, Andrew & Underwood 1992, Johnson et al.

2005), New Zealand (Naylor & Gerring 2001), and California (Karpov et al. 1998). Hypotheses to explain negative associations between *C. rodgersii* and *H. rubra* include competition for food (Shepherd 1973, Strain & Johnson 2009, Chapter 3) and shelter (Andrew et al. 1998), and losses to predators as a result of competitive displacement from shelter (Lowry & Pearce 1973). However the effects of competitive between *C. rodgersii* and *H. rubra* in intact algal beds have not been tested.

Separating the effects and relative magnitude of intra- and interspecific competition between *C. rodgersii* and *H. rubra* may have important implications for the large scale dynamics of these reef systems and the fisheries they support. If *C. rodgersii* is the superior competitor in interactions with *H. rubra,* then the establishment of this urchin may have a negative impact on the abundances of abalone and/or their accessibility to fisheries. Alternatively, if *H. rubra* is the superior competitor in interactions with *C. rodgersii,* then fishing of abalone may lead to an increase in the distribution and abundance of the urchin with a concomitant increase in the risk of barrens formation. Broader scale effects on system dynamics may also arise if competition affects levels of aggression, avoidance behaviours and dispersal, or stimulates the use of a wider variety of food and habitats (Branch 1975, Byers 2000a), or affects the risk of predation to realise complex interactions between competition and predation (Iribarne et al. 1994). However, the effects of competition on behavioural and movement responses are rarely explored because of sampling and analysis difficulties, especially in detecting impacts (Byers 2000b, Lusseau 2003).

We used experimental additions of urchins and removals of abalone to test the effects of (i) interspecific interactions between *C. rodgersii* and *H. rubra,* (ii) intraspecific interactions in *H. rubra,* (iii) the translocation procedures on *C. rodgersii* and (iv) the tagging procedures on *H. rubra,* behavioural transitions, movement patterns and local abundances of urchins and abalone in intact algal beds.

MATERIALS AND METHODS

Site characteristics

Experiments were conducted on subtidal reefs at two sites, *viz.* Magistrate's Point, and the Lanterns, ~60 km apart on the east coast of Tasmania, June 2005 to March 2006 (Figure 1). Both sites support a variety of habitat types,

ranging from urchin barrens patches to areas dominated by diverse stands of canopy-forming algal with well-developed understorey.

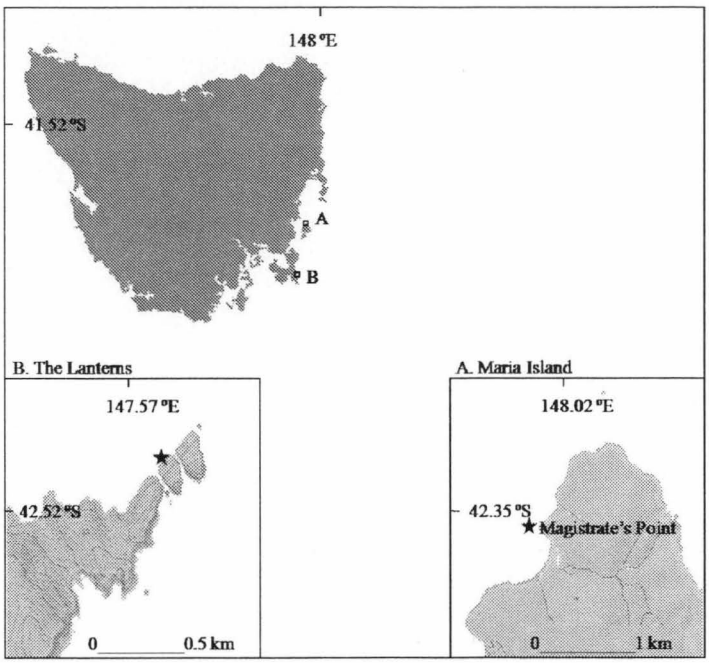

Figure 1. Map of the east coast of Tasmania, Australia, showing the locations, the Lanterns and Magistrate's Point, Maria Island of the study sites.

We tested the effects of interspecific competition between *Centrostephanus rodgersii* and *Haliotis rubra* at Magistrate's Point, in the Maria Island marine reserve, to avoid confounding with any effects of fishing abalone. The reserve supports high densities of *H. rubra,* but very low densities of *C. rodgersii,* relative to the surrounding fished areas (Edgar & Barrett 1999). The site is characterised by a gently sloping rocky substratum to a depth of ~11 m and is moderately sheltered from all but south-westerly swells (Edgar 1984).

All *C. rodgersii* used in the experiments at Magistrate's Point were collected from the Lanterns. To test the effect of the translocation procedures on *C. rodgersii,* an experiment was also conducted at the Lanterns. This site is characterised by steeply sloping rocky substratum to a depth of ~41 m and supports a relatively high density of *C. rodgersii* and patches of barrens

habitat. The site is moderately exposed to easterly swells which, although infrequent, can be large (Edgar 1984)

At both sites the distribution, abundances, and size range of *C. rodgersii* and *H. rubra* were determined from a sample of 20, 3x3 m quadrats, positioned randomly in 3-13 m water. The mean abundance and size range of *C. rodgersii* was 18 individuals per 9 m^2 (+/- 0.98 SE), with test diameter ranging between 90-125 mm. The mean abundances and size range of *H. rubra* was 25 individuals per 9 m^2 (+/- 0.95 SE), with shell length ranging between 90-190 mm. Animals were measured using vernier callipers. All experiments were conducted in 7-11 m waters where the distribution of *C. rodgersii* and *H. rubra* overlapped.

Experimental design

Experimental manipulations were conducted in 3x3 m open plots. All plots were marked with 5 star pickets, 1 in each corner and 1 in the centre of the plot. Initial assessments were undertaken by eye to ensure that the cover of the substratum (large boulders, small boulders, and sand) algae (brown, green, red) and sessile invertebrates and the density of benthic invertebrates (urchins and gastropods) were broadly consistent between plots, at Magistrate's Point and the Lanterns.

Tagging *C. rodgersii* and *H. rubra*

Throughout the series of experiments, we tagged all *C. rodgersii* and *H. rubra,* excluding the animals in the tagging controls. *H. rubra* were tagged by divers *in situ,* at Magistrate's Point. Abalone shells were scrubbed with a copper wire brush and leader sheep ear tags (12x2 mm) were glued to the shell with epoxy resin (Z-spar A-788), mixed just prior to diving. *C. rodgersii,* were collected at the Lanterns and tagged immediately on the dive vessel, using a modification of the methods described by Pederson and Johnson (2006). Two holes were made in the test, using a 1.25 mm diameter hypodermic needle. The needle passed through the test close to the maximum ambital radius between the oral and aboral surface. Monofilament fishing line (0.5 mm diameter) was then threaded through the hypodermic needle, which was then removed. Colour-coded beads were threaded over the monofilament line in individual combinations to uniquely identify each animal before the line was closed as a loop by crimping with a stainless steel number 4-size Leader sleeve. In the experiments at Magistrate's Point, tagged *C. rodgersii* were transported by car and boat, in ~3 hours and placed

into cages, where they were held for 1 week before being transferred randomly into plots. In the experiment at the Lanterns, tagged *C. rodgersii* were kept out of water in the boat for the amount of time before being released into plots.

Experimental manipulations

We used a series of experimental manipulations (n=3) to test the effects of interspecific competition and the translocation procedures on *C. rodgersii* and the effects of intra- and interspecific competition and the tagging procedure on *H. rubra* (Table 1 & 2).

Experiment 1: Effect of interspecific competition

To test the effect of interspecific competition on the behavioural transitions, movement patterns and resightability of *C. rodgersii* and *H. rubra* in winter of 2005, the following treatments were applied to plots at Magistrate's Point.

Treatment 1:1x ambient density *C. rodgersii* were added randomly to plots where all *H. rubra* had been removed (1U0A)

Treatment 2:1x ambient density *C. rodgersii* were added randomly to plots with 1x ambient density of *H. rubra* (1A1U)

Treatment 3:1x ambient density of *H. rubra* (1A)

The assessments took place immediately prior to, and 1 day, 1 week, 2 weeks and 4 weeks after manipulations. Because there were no detectable effects of interspecific competition on *C. rodgersii,* subsequent experiments focused on testing the effect of intra- and interspecific competition on *H. rubra*

Experiment 2: Effects of intra- and interspecific competition

To test the effects of intra- and interspecific competition on the behavioural transitions, movement patterns and resightability of *H. rubra* in summer of 2006, the following treatments were applied to plots at Magistrate's Point.

Treatment 1:1x ambient density of tagged *H. rubra* (1A)

Treatment 2:2x ambient density of tagged *H. rubra* (1A1A)

Treatment 3:1x ambient density of tagged *H. rubra* with 1x ambient density *C. rodgersii* (1A1U)

Table 1. *Centrostephanus rodgersii* and *Haliotis rubra.* Treatments involving manipulations of *C. rodgersii* and *H. rubra* densities in 9 m^2 open plots. Ambient densities of *C. rodgersii* (1U) and *H. rubra* (1A) were ~18 urchins and ~25 abalone.

Treatment	Manipulation
Experiment 1: Effect of interspecific competition on *C. rodgersii* and *H. rubra*	
1U0A	1x ambient density of *C. rodgersii* where all *H. rubra* were removed
1A1U	1x ambient density of *H. rubra* with 1x ambient density of *C. rodgersii*
1A	1x ambient density of *H. rubra*
Experiment 2: Effect of intraspecific and interspecific competition on *H. rubra*	
1A	1x ambient density of tagged *H. rubra*
1A1A	2x ambient density of tagged *H. rubra*
1A1U	1x ambient density of *H. rubra* with 1x ambient density of *C. rodgersii*
Experiment 3: Effect of translocation procedures on *C. rodgersii*	
1	1x ambient density of untagged and undisturbed *C. rodgersii* were left in plots at the Lanterns
2	1x ambient density of tagged *C. rodgersii* replaced back into the same positions and plots they were collected at the Lanterns
3	1x ambient density of tagged *C. rodgersii* placed in random positions into the same plots they were collected at the Lanterns
4	1x ambient density of *C. rodgersii* were placed randomly into new plots at the Lanterns
5	1x ambient density of *C. rodgersii* were placed randomly into new plots at Magistrate's Point
Experiment 4: Effect of tagging on *H. rubra*	
1	1x ambient density of tagged *H. rubra*
2	1x ambient density of untagged and undisturbed *H. rubra*

Table 2. *Centrostephanus rodgersii* and *Haliotis rubra.* Details of the planned comparisons to test the effect of interspecific competition and translocation procedures on resightability and movement patterns of *C. rodgersii* and the effect of intra- and interspecific competition, and the tagging procedure on the resightability and movement patterns of *H. rubra.* Ambient densities of *C. rodgersii* (1U) and *H. rubra* (1A) were ~18 urchins and ~25 abalone.

Comparisons	Rationale
Experiment 1: Effect of interspecific competition on *C. rodgersii* and *H. rubra*	
1U0A vs. 1A1U	Effect of interspecific competition on *C. rodgersii* behaviour and movement day 1, week 1, 2, 4
1A1U vs. 1A	Effect of interspecific competition on *H. rubra* behaviour and movement day 1, week 1, 2, 4
Experiment 2: Effect of intra- and interspecific competition on *H. rubra*	
1A1A vs. 1A1A	Effect of intraspecific competition on resightability of *H. rubra* weeks 1-3 vs. 4-6, 1-3 vs. 7-9
1A1U vs. 1A	Effect of interspecific competition on resightability of *H. rubra* weeks 1-3 vs. 4-6, 1-3 vs. 7-9
1A1A vs. 1A1U	Effect of interspecific competition relative to intra- competition on resightability of *H. rubra* weeks 4-6
1A vs. 1A1A	Effect of intraspecific competition on movement patterns of *H. rubra* week 4, 5, 6
1A vs. 1A1U	Effect of interspecific competition on movement patterns of *H. rubra* week 4, 5, 6
1A1A vs. 1A1U	Effect of intra- versus interspecific competition on movement patterns of *H. rubra* week 4, 5, 6
Experiment 3: Effect of translocation procedures on *C. rodgersii*	
1 vs. 2	Effect of Tagging of *C. rodgersii*
2 vs. 3	Effect of changing *C. rodgersii* position in the plot
3 vs. 4	Effect of transferring *C. rodgersii* into new plots at the Lanterns
4 vs. 5	Effect of transferring *C. rodgersii* into new plots at the Magistrate's Point
Experiment 4: Effect of tagging procedure on *H. rubra*	
1 vs. 2	Effect of tagging *H. rubra*

Extra *H. rubra* for treatment 2 were collected approximately 100 m away from the site, tagged with orange crayon (which lasted the duration of the experiment) and placed randomly into plots. We did not monitor the responses of the extra abalone throughout the experiment. The assessments took place immediately prior to manipulations and then weekly for 9 weeks. In this experiment, weeks 1 to 3 were preceding treatment, weeks 4 to 6 were during treatment (i.e. with added *C. rodgersii* or extra *H. rubra*), and weeks 7 to 9 were after the cessation of the treatment (when added *C. rodgersii* and extra *H. rubra* had been removed), however distances moved by *H. rubra* were only measured during weeks 4 to 6.

Experiment 3: Effects of the translocation procedures on *C. rodgersii*

To test the effect of interspecific competition on *C. rodgersii,* it was necessary to translocate urchins from the Lanterns to Magistrate's Point. To test effect of the translocation procedures on the resightability of *C. rodgersii,* in winter of 2005, the following treatments were applied to plots at the Lanterns and Magistrate's Point.

Treatment 1: 1x ambient density of untagged and unmanipulated *C. rodgersii* were left in plots at the Lanterns

Treatment 2: 1x ambient density of tagged *C. rodgersii* were placed back into the same positions and plots where they were collected at the Lanterns

Treatment 3: 1x ambient density of tagged *C. rodgersii* were placed in random positions into the same plots where they were collected at the Lanterns

Treatment 4: 1x ambient density of tagged *C. rodgersii* were placed randomly into new plots at the Lanterns

Treatment 5: 1x ambient density of *C. rodgersii* were placed randomly into new plots at Magistrate's Point

The assessments took place immediately prior to, and 1 day, 1 week, 2 weeks and 4 weeks after manipulations.

Effects of tagging procedure on *H. rubra*

To test the effects of the tagging procedure on the resightability of *H. rubra,* in the winter of 2005, the following treatments were applied to plots at Magistrate's Point.

Treatment 1:1x ambient density of tagged *H. rubra*

Treatment 2:1x ambient density of untagged *H. rubra*

The assessments took place immediately prior to, and 1 day, 1 week, 2 weeks and 4 weeks after manipulations.

Response variables

For all experiments, the number and identity of predators (fishes and rock lobsters) in the area inside each 3x3 m plot and 1 m outside the plot were recorded. We then searched the area inside the plots (for tagged and untagged *C. rodgersii* and *H. rubra*) and 1 m area outside the plot (for tagged abalone and urchins) for 1 hour. We recorded the identity and total number of all tagged *C. rodgersii* and *H. rubra* (including dead animals) inside and 1 m outside the plot and the number of untagged *C. rodgersii* and *H. rubra* inside the plot. In the experiments designed to test the effect of interspecific competition on *C. rodgersii* and the effects of intra- and interspecific competition on *H. rubra,* microhabitat use by urchins and abalone, inside each plot was recorded as either, exposed (out in the open) or sheltered (in a crevice, or under a rock, or sitting vertically against or under a rock). Animals 1 m outside the plots were recorded as being outside and tagged animals that were not relocated were classified as lost. The position of individual *C. rodgersii* and *H. rubra* inside plots was determined by triangulation based on the distances to the 2 nearest star pickets, and noting which picket was on the right hand side. Movement of *C. rodgersii* and *H. rubra* was described by their change in position on consecutive visits to plots.

Data analysis

Resightability

The effect of interspecific competition and the translocation procedures on the percentage of *C. rodgersii* and the effects of intra- and interspecific competition and the tagging procedures on the percentage of *H. rubra* resighted through time were analysed with 2-way univariate repeated measures ANOVA. We used the Greenhouse-Geisser adjusted degrees of freedom when data did not meet the assumption of sphericity.

To test the effects of interspecific competition on *C. rodgersii,* the model included the main effect of treatment (fixed, 2 levels=1U0A, 1A1U) and time (random, 4 levels=1 day and 1, 2, and 4 weeks). Similarly, to test the effect of interspecific competition on *H. rubra,* the model include the main effects of treatment (fixed 2 levels=1A, 1A1U) and time (random, 4 levels=1 day and 1, 2, and 4 weeks). To test the effects of intra- and interspecific

competition on *H. rubra,* the model included the main effects of treatment (fixed, 3 levels=1A, 1A1A, 1A1U) and time (random, 9 levels=weeks 1 to 9).

To test the effect of the translocation procedures on *C. rodgersii,* the model included the main effects of treatment (fixed, 5 levels=5 treatments) and time (random, 4 levels=1 day, and 1, 2 and 4 weeks). To test the effect of the tagging procedures on *H. rubra,* the model included the main effect of treatment (fixed, 2 levels=2 treatments) and time (random, 4 levels=1 day and 1, 2, and 4 weeks).

Behavioural transitions

The effect of interspecific competition on *C. rodgersii* and intra- and interspecific competition on *H. rubra* behavioural transitions (the probability of changing from one behavioural state to another) were analysed using Markov chain modelling (Markov 1971, Lusseau 2003). Markov chains quantify the dependence of behaviour on preceding behaviour. There are several degrees of dependence, if sequenced behaviours are independent they are described by a zero-order Markov chain. If a particular behaviour depends only on the behaviour immediately preceding it, then a first-order Markov chain is fitted, and so on. Here we used a first-order Markov chain to model the time dependence of behaviour, while retaining a relatively simple analytical design. We tested between the zero- and first-order chains for the control animals using a χ^2 likelihood ratio test.

To create the first order Markov chain model, we used a log linear regression model with a multinomial error distribution. The response variable for this model was the behavioural state of individual *C. rodgersii* and *H. rubra* (exposed (E), sheltered (S), lost (L) and outside the plot (O)), at all time points, except the first. The model included the main effects of *C. rodgersii* and *H. rubra* behaviour in the immediately preceding time point, treatment, and plot and their interaction. In the experiment testing the effects of interspecific competition on *H. rubra* and *C. rodgersii*, there were no detectable effect of plot in the controls and so plot was removed from the model. However in the experiment testing the effect of intra- and interspecific competition on *H. rubra,* plot was significant and so results presented were adjusted for this plot affect.

To test the assumption that the behaviour in the control animals remained the same over time, we included time in the model. A χ^2 likelihood ratio test was used to test between models with and without time.

Transition probabilities (through time) were then determined for *C. rodgersii* and *H. rubra* from the regression coefficients of the log-linear model, using the following transformation:

$$p_{ij} = \frac{\beta_{ij}}{\sum_{k=(E,L,O,S)} \beta_{ik}}$$

where i is the preceding behaviour, j is succeeding behaviour (i and j could include any of the four behavioural states). β_{ij} is the coefficient for the ith behaviour of the outcome variable and jth behaviour of the dependent variable, and p_{ij} is the transition probability from i to j in the Markov chain. Each behavioural transition is equivalent to the proportion of time that the specific behaviour was observed. The effect of interspecific competition on *C. rodgersii* and intra- and interspecific competition on *H. rubra* behaviour-transition probability matrices were tested using a χ^2 likelihood ratio test. A proportions test was used to test for the effect of treatments on specific behavioural transitions.

Movement patterns

Distances moved by individual *C. rodgersii* and *H. rubra* could not be assumed to be independent through time. These data were summed through time, for each plot. The effects of interspecific competition on *C. rodgersii* and intra- and interspecific competition on *H. rubra* mean distanced moved were analysed with a 1-way fixed factor Kruskal-Wallis test (see resightability section for model details).

To obtain a measure of the error inherent in the methods used for determining distances moved by *C. rodgersii* and *H. rubra,* distances between the 8 pairs of reference markers were measured ten times (mean=0.1 m, SE=+/-0.012 m). There was high precision in our measurements of distances moved by *C. rodgersii* and *H. rubra.*

To test the effect of interspecific competition on the distances moved by *C. rodgersii* and the effect of intra- and interspecific competition on distances moved by *H. rubra,* all movement data was plotted onto histograms (Figure

2). This graph demonstrated that the majority of animals moved distances 0-0.6 m, although some moved much greater distances. Thereafter, we labelled animals that moved ≤0.4 m homing (61.35% *C. rodgersii* and 77.74% *H. rubra*), and those that moved >0.4 m were deemed mobile (38.65% *C. rodgersii* and 22.26% *H. rubra*). We also tested other definitions of homing (≤0.2 m and ≤0.6 m) and mobile (>0.2 m and 0.6 m) *C. rodgersii* and *H. rubra,* which had no effect on our biological conclusions.

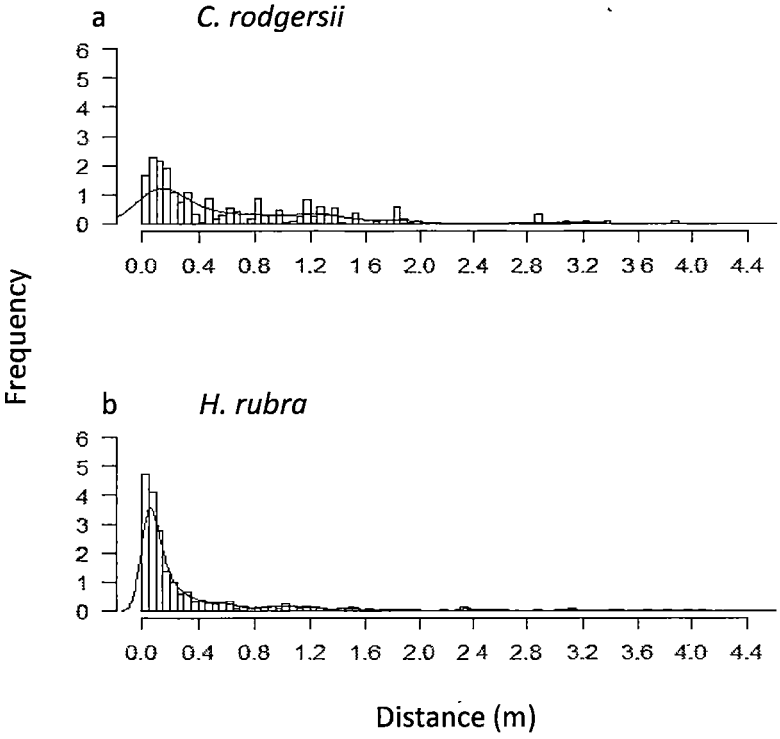

Figure 2. *Centrostephanus rodgersii* and *Haliotis rubra.* Frequency plots of distances (m) moved by (a) *C. rodgersii* and (b) *H. rubra.* Bar widths are 0.05 m. The continuous line shows the probability function that describes best the distribution of the data.

To test effects of interspecific competition on *C. rodgersii* and *H. rubra* (day 1 and weeks 1, 2 and 4) and intra- and interspecific competition *H. rubra* (weeks 4, 5, 6) we examined the proportion of homing and mobile individuals, at each time interval with G-tests. To test for the effects of interspecific competition on *C. rodgersii* and *H. rubra,* 2x2 G-tests were used. To test the effects of intra- and interspecific competition on *H. rubra,* 3x2 G-tests were used and when significant differences were observed, these

were followed by 2x3 G-tests. To compensate for increased type I error and low numbers, Williams's corrections (q) were applied in all G-tests.

Predators

It could not be assumed that predator densities were independent through time. The densities of southern rock lobster (*Jasus edwardsii*) and fish (*Pictilabrus laticlavius, Notolabrus tetricus, Notolabrus fucicola* and *Latridopsis forsteri*) were summed through time, for each plot. The differences in the densities of predators between treatments were analysed using 1-way ANOVAs (see above resightability section for model details).

For all parametric ANOVAs, the relationship between the standard deviation and means of the densities was used to determine the appropriate transformation to stabilise variances. Transformed data were checked for both normality (using normal probability plots) and homoscedasticity. Transformations are expressed in terms of the raw dependent variable, Y. For repeated measure ANOVAs, the Mauchly's test of sphericity was also used to test the correlation structure.

For all analyses where significant differences were found, planned comparisons were conducted between treatments (Table 2). Where comparison sets were non-orthogonal, the significance level was adjusted using Todd & Keough (1994). All statistical analyses and graphics were undertaken using R.

RESULTS

Percentage resighted

In total, 108 *Centrostephanus rodgersii* and 693 *Haliotis rubra* were monitored throughout the experiments. There were no detectable effects of the translocation procedures or of interspecific competition on the percentage of *C. rodgersii* resighted through time (Table 3). There were also no detectable effects of the tagging procedure on the percentage of *H. rubra* resighted through time (Table 4).

Table 3. *Centrostephanus rodgersii.* Results of 2-way repeated measures ANOVA testing the effect of interspecific competition and translocation procedures on the percentage of *C. rodgersii* resighted at Magistrate's Point, Maria Island and the Lanterns. Significant p-values are indicated in bold print: $p < 0.05$.

Sources of variation	df	MS	*F*	p
Interspecific competition				
Treatment	1	1.5	0.127	0.74
Error	4	11.84		
Time	4	15.278	12.5	**0.003**
Treatment x Time	4	0.167	0.136	0.936
Error	16	1.222		
Translocation procedure				
Treatment	3	454.39	3.141	0.087
Error	8	144.676		
Time	3	103.414	1.791	0.109
Treatment x Time	12	57.756		
Error	24			

In contrast, interspecific but not intra- competition resulted in a significant reduction in the percentage of *H. rubra* resighted through time (Figure 3, 4, Tables 4). In the experiment testing the effect of interspecific competition, additions of *C. rodgersii* lead to significant declines in the percentage of *H. rubra* resighted, in weeks 1, 2 and 4 when compared with the control without urchins. However there were no detectable effects of interspecific competition on the percentage of abalone resighted 1 day after urchins were added. In the experiment testing the effects of intra- and interspecific competition there were no detectable differences in the percentage of abalone resighted through time in the control or the treatment with added extra abalone. However, additions of *C. rodgersii* resulted in a decline in the percentage of abalone resighted (weeks 4 to 6 with urchins) and weeks 7 to 9 (after urchins were removed) compared with the control weeks 1 to 3 (prior to the addition of urchins). Inter- rather than intraspecific competition explained the significant decline in the percentage of *H. rubra* resighted through time.

Table 4. *Haliotis rubra.* Results of 2-way repeated measures ANOVA testing the effect of intra- and interspecific competition and tagging on the percentage of *H. rubra* resighted. Significant p-values are shown in bold print: $p<0.05$ main analysis and $p<0.0125$ planned comparisons testing the effect of interspecific competition, $p<0.007$ planned comparisons testing the effect of intra- and interspecific competition (α adjusted using Todd & Keough (1994)).

Factors	**df**	**MS**	***F***	**p**	**Comparisons**	***F***	**p**
Interspecific competition							
Treatment	1	1539.4	18.501	**0.013**	1A vs.1A1U day1	2.99	0.159
Error	4	83.206			1A vs.1A1U week 1	40.913	**0.003**
Time	2.082	304.872	5.163	**0.034**	1A vs.1A1U week 2	15.814	**0.01**
Treatment x Time	2.082	179.839	3.045	0.101	1A vs.1A1U week 4	10.61	**0.01**
Error	8.328	59.055					
Intra- and interspecific competition					1A weeks 1-3 vs. weeks 4-6	4.192	0.06
Treatment	2	1386.289	3.010	0.124	1A weeks 1-3 vs. weeks 7-9	3.828	0.07
Error	6	460.569			1A1U weeks 1-3 vs. weeks 4-6	16.941	**0.001**
Time	2.958	1509.364	15.380	**$<2e^{-16}$**	1A1U weeks 1-3 vs. weeks 7-9	22.299	**$<2e^{-16}$**
Treatment x Time	5.915	398.702	4.063	**0.01**	1A1A weeks 1-3 vs. weeks 4-6	10.868	0.01
Error	17.746	98.141			1A1A weeks 1-3 vs. weeks 7-9	7.819	0.02
Tagging procedure					1A1U weeks 4-6 vs. weeks 4-6	43.898	**$<2e^{-16}$**
Treatment	1	45.594	0.762	0.432			
Error	4	59.865					
Time	1.89	221.668	3.291	0.0.95			
Treatment x Time	1.89	66.365	0.985	0.412			
Error	7.598	67.349					

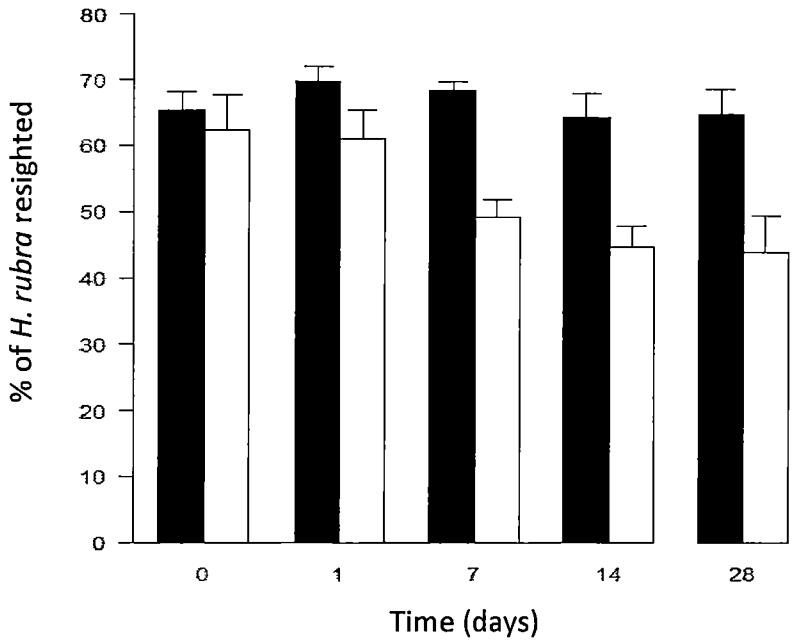

Figure 3. *Haliotis rubra.* Effects of interspecific competition on the percentage of tagged abalone resighted through time (days), at Magistrate's Point, Maria Island (see Table 4 ANOVA results). Data are the means (+/- SE) of *n*=3 replicates. Treatments are 1A=1x ambient density of *H. rubra* (unshaded bars) and 1A1U=1x ambient density of *H. rubra* with 1x ambient density of *C. rodgersii* (shaded bars). There were significant differences between treatments from day 7 onwards (see Table 4 results).

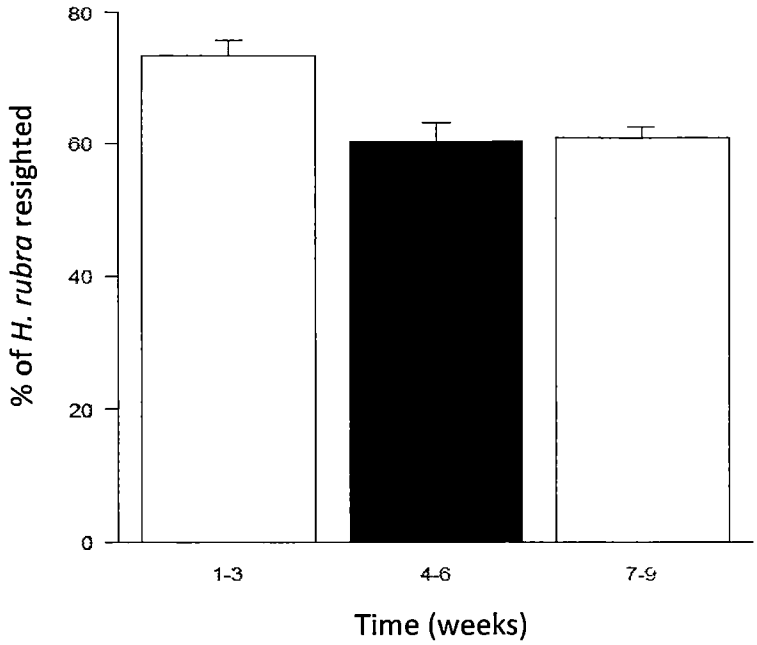

Figure 4. *Haliotis rubra.* Effect of interspecific competition on the percentage of tagged abalone resighted through time (weeks), at Magistrate's Point, Maria Island. Data means (+/-SE) of n=3 replicates. Unshaded bars are 1A=1x ambient densities of *H. rubra* (weeks 1-3 preceding the addition of urchins and weeks 7-9 when urchins were removed) and shaded bars and 1A1U=1x ambient densities of *H. rubra* with 1x ambient densities of *C. rodgersii* (weeks 4-6 with added urchins). There were significant differences between weeks 1-3, weeks 4-6 and weeks 7-9, (see Table 4 results).

Behavioural transitions

Divers spent 99 hours underwater monitoring the behaviour of 54 *C. rodgersii* and 495 *H. rubra*. In the control plots, *H. rubra* behaviour remained very consistent through time. Additions of *C. rodgersii* resulted in immediate, significant and consistent changes to *H. rubra* behaviour. In contrast, additions of extra abalone resulted in slower and inconsistent changes to *H. rubra* behaviour.

Transitions in the behavioural states of *C. rodgersii* ($\chi^2_{24, 981}$=13.1, p=0.97) and *H. rubra* (interspecific competition experiment, $\chi^2_{33,1179}$=43.0, p=0.11 and intra- and interspecific competition experiment $\chi^2_{5,1722}$=0.78, p=0.85) in control treatments were stable over time and first-order transitions provided more information than zero-order chains (interspecific competition experiment, urchins, $\chi^2_{9,1179}$=108.5, p<2e-16 and abalone $\chi^2_{9,1212}$=534.4, p<2e-16, and intra- and interspecific competition experiment abalone, $\chi^2_{60,1725}$=378.7, p<2e-16).

There were no detectable effects of interspecific competition on *C. rodgersii* behavioural transitions ($\chi^2_{15, 981}$=8.71, p=0.67). In contrast, addition of *C. rodgersii* or extra abalone lead to changes in *H. rubra* behavioural transitions in both experiments (interspecific competition experiment, $\chi^2_{12, 2412}$=21.3, p=8e-5, intra- and interspecific competition experiment additions of urchins $\chi^2_{3, 927}$=17.68, p=5e-4 and extra abalone $\chi^2_{3, 813}$=14.138, p=8e-4).

Addition of *C. rodgersii* impacted on four *H. rubra* behavioural transitions (Figures 4, 5). In both experiments, two behavioural transitions (remaining sheltered and moving from exposed→ sheltered) increased in frequency, while two transitions remaining exposed and sheltered→ exposed) became less frequent. The magnitudes of the differences in transition probabilities between control and treatment chains varied through time. The relative probability of *H. rubra* remaining exposed almost halved within a week of adding *C. rodgersii* to plots, and remained low while the urchins were present, when compared to control plots with no urchins. The probability of *H. rubra* changing behaviour from exposed→ sheltered doubled within a week after *C. rodgersii* were added to plots, and remained consistently high. The probability of *H. rubra* changing behaviour from sheltered→ exposed initially decline after addition of *C. rodgersii* but then increased.

In the interspecific competition experiment, the probability of *H. rubra* remaining sheltering increased from 78% to 97% within a day of adding *C. rodgersii* to plots and then remained consistently higher than the control plots with no urchins. In the intra- and interspecific competition experiment, the probability that *H. rubra* remained sheltering increased from 78% to 88% within a week of adding *C. rodgersii* and then remained consistently high.

Increasing the density of abalone in plots changed three *H. rubra* behavioural transitions (Figure 6). The likelihood of abalone remaining exposed decreased, while the likelihood of remaining sheltering and moving from sheltered→ lost increased. One week after extra conspecifics were added to plots the probability of *H. rubra* remaining sheltered dropped from 86% to 65% and remained consistently low throughout the experiment while the probability of *H. rubra* changing from sheltered→ lost increased to from 16% to 24% and remained consistently high throughout the experiment. Two weeks after conspecifics were added to plots the probability of *H. rubra* remaining exposed almost halved from 82% to 38% and remained at this low level for the duration of the experiment.

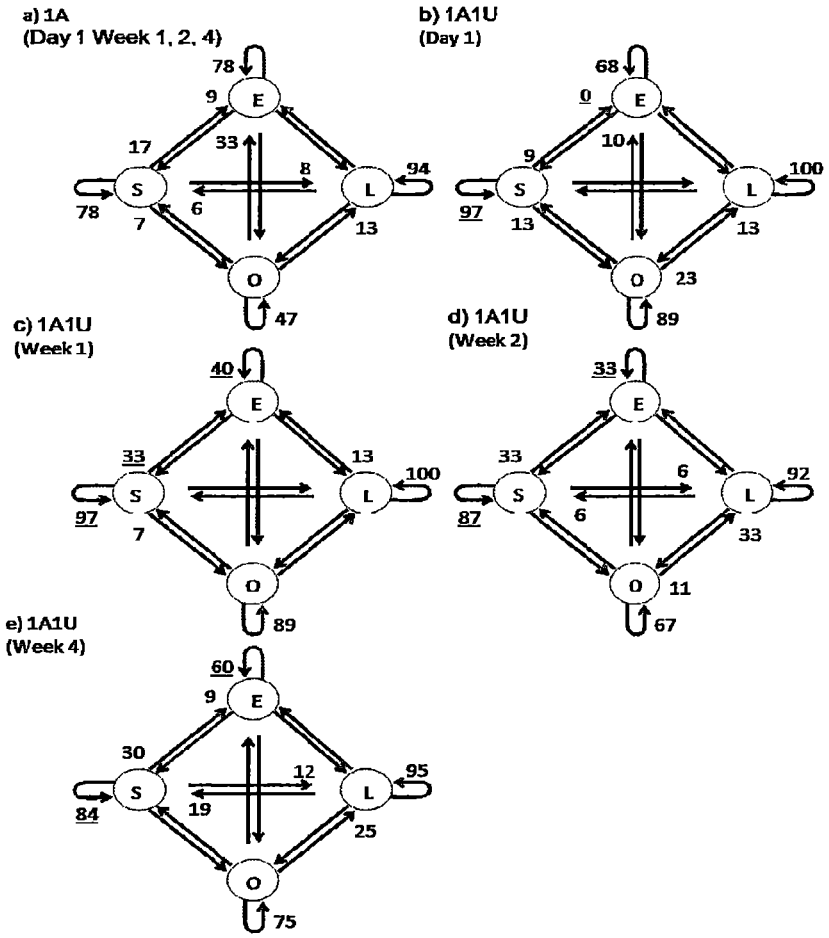

Figure 5. *Haliotis rubra.* Effect of interspecific competition on *H. rubra* behavioural transitions at Magistrate's Point, Maria Island. Data are the percentage of *H. rubra* in each behavioural state (E=exposed, L=lost, O=outside the plot, S=sheltered). Treatments are (a) 1A=1x ambient density of *H. rubra*, with all times combined (day 1 and weeks 1, 2 and 4), (b) 1A1U=1x ambient density of *H. rubra* with 1x ambient density of *C. rodgersii,* 1 day after the addition of urchins, (c) 1A1U, 1 week after the addition of urchins (d) 1A1U, 2 weeks after the addition of sea urchins and (e) 1A1U, 4 weeks after the addition of urchins. Transitions that are significantly impacted by the addition of urchins are underlined. Only percentages >5 are shown.

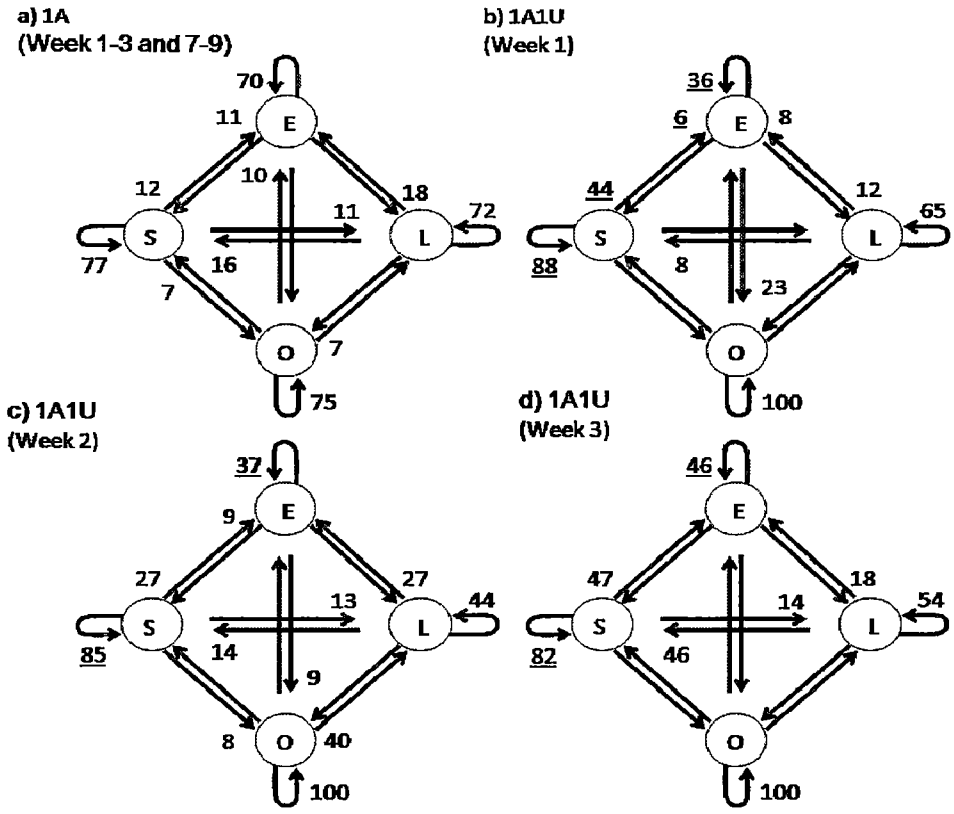

Figure 6. *Haliotis rubra.* Effect of interspecific competition on *H. rubra* behavioural transitions at Magistrate's Point, Maria Island. Data are the percentage of *H. rubra* in each behavioural state (E=exposed, L=lost, O=outside the plot and S=sheltered). Treatments are (a) 1A=1x ambient density of *H. rubra*, all times combined (weeks 1 to 3 and 7 to 9), (b) 1A1U=1x ambient density of *H. rubra* with 1xambient density of *C. rodgersii*, 1week after the addition of urchins, (c) 1A1U, 2 weeks after the addition of urchins, and (d) 1A1U, 3 weeks after the additions of urchins. Transitions significantly impacted by addition of urchins are underlined. Only percentages >5 are shown.

Movement patterns

There were no detectable effects of interspecific competition on the mean net distances moved by *C. rodgersii* ($\chi^2_{1,9}$=239.11, p=0.56). In contrast, both intra- and interspecific competition resulted in a significant increase in the mean net distance moved by *H. rubra* (interspecific competition experiment, $\chi^2_{1,981}$=11.176, p=8e-4 and intra- and interspecific competition experiment, $\chi^2_{2,981}$=55.36, p=9e-13). There was no detectable difference in the effects of intra- and interspecific competition on mean the net distances moved by *H. rubra* ($\chi^2_{1,981}$=1.183, p=0.277, $\alpha_{adjusted}$=0.017).

Intra- and interspecific competition had a significant effect on the proportion of homing and mobile *H. rubra* (Figures 7, 8, Tables 5). In the interspecific competition experiment, additions of *C. rodgersii* resulted in an increase in the proportion of mobile *H. rubra* in weeks 1, 2 and 4 after the addition of urchins, compared with control. In the intra and interspecific competition experiment, additions of *C. rodgersii* similarly resulted in an increase in the proportion of mobile *H. rubra* in weeks 4, 5 and 6 during treatment when compared with the control. Additions of extra conspecifics also led to increases in the proportion of mobile *H. rubra,* in weeks 5 and 6, when compared with the control. However there were no detectable effects of extra conspecifics on the proportion of mobile *H. rubra* in week 4. There was no detectable difference in the effect of intra- and intraspecific competition on the proportion of mobile and homing *H. rubra* in weeks 4, 5 and 6.

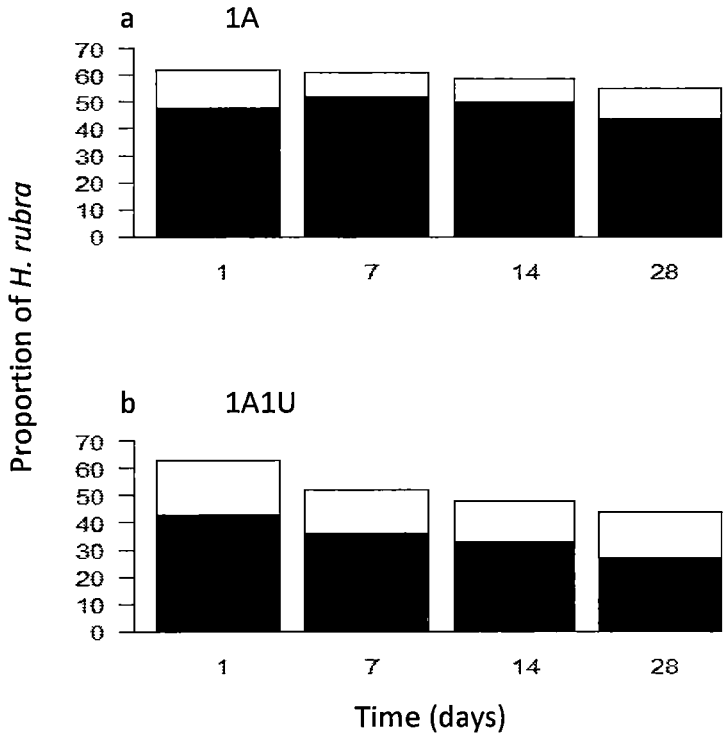

Figure 8. *Haliotis rubra.* Effect of interspecific competition proportion of homing (unshaded bars=net distance moved <0.4 m) and mobile (shaded bars=net distances moved ≥0.4m) abalone through time (days) at Magistrate's Point, Maria Island. Treatments are (a) 1A=1x ambient density of *H. rubra*, and (b) 1A1U=1x ambient density of *H. rubra* with 1x ambient density of *C. rodgersii.* There were significant differences in the proportion of homing and mobile *H. rubra* between treatments from day 7 onwards (see Table 5 for results).

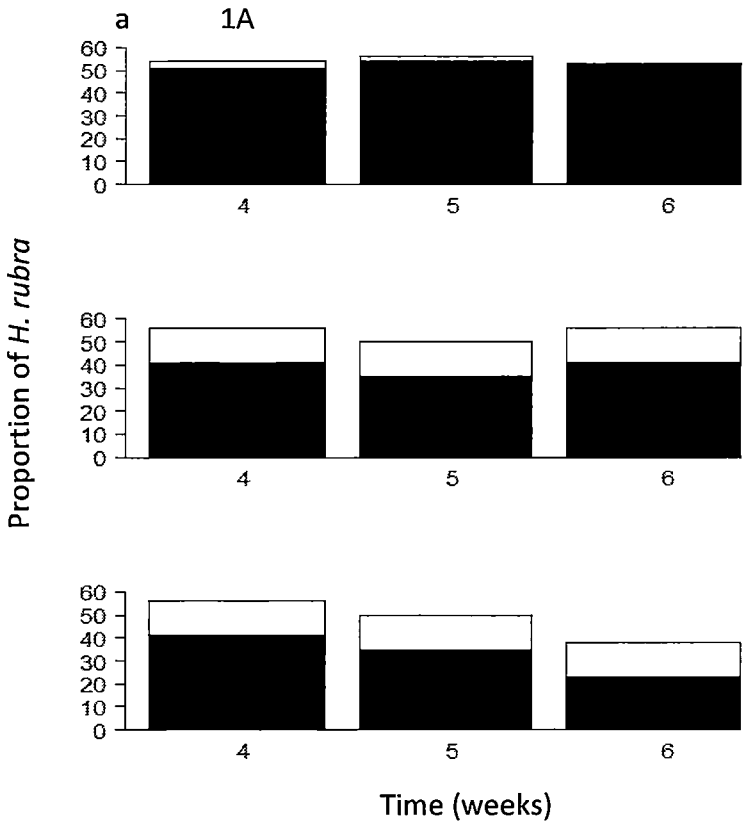

Figure 9. *Haliotis rubra.* Effect of intra- and interspecific competition on proportion of homing (unshaded bars=net distance moved <0.4 m) and mobile (shaded bars=net distances moved ≥0.4m) abalone through time (weeks) at Magistrate's Point Maria Island. Treatments are (a) 1A=1x ambient density of *H. rubra*, (b) 1A1U=1x ambient density of *H. rubra* with 1x ambient density of *C. rodgersii,* and (c) 1A1A=2x ambient density of *H. rubra.* There were significant differences between 1A vs. 1A1A in weeks 5 and 6 and between 1A vs. 1A1U in weeks 4, 5 and 6 (see Table 5 for G-test results).

Table 5. *Haliotis rubra.* Result of log-linear models testing the effect of interspecific and intra- and interspecific competition on the proportion of homing (≤0.4m) and mobile (≥0.4m) abalone in experiments at Magistrate's Point, Maria Island. Significant p-values are shown in bold print: $p<0.05$ are significant for the main analysis and $p<0.0125$ are significant comparisons testing the effect of interspecific competition and $p<0.005$ are significant comparisons testing the effect of intra- and interspecific competition (α adjusted using Todd & Keough (1994)).

Factors	df	Log likelihood	p	Comparisons	Log likelihood	p
Interspecific competition						
Treatment	1	15.865	**0.027**	1A vs.1A1U day 1	2.314	0.128
				1A vs.1A1U week 1	5.746	**0.01**
				1A vs.1A1U week 2	6.541	**0.01**
				1A vs.1A1U week 4	6.917	**0.008**
Intra- and interspecific competition						
Treatment	2	69.732	**0.001**	1A vs. 1A1U week 4	10.31	**0.002**
				1A vs. 1A1U week 5	8.846	**0.002**
				1A vs. 1A1U week 6	15.685	**$7e^{-5}$**
				1A vs. 1A1A week 4	5.79	0.01
				1A vs. 1A1A week 5	10.134	**0.001**
				1A vs. 1A week 6	16.964	**$3e^{-5}$**
				1A1A vs. 1A1A week 4	0.136	0.713
				1A1A vs. 1A1U week 5	0.07	0.8
				1A1A vs. 1A1U week 6	0.734	0.39

Predators

The number of predators associated with the experimental plots remained consistently low throughout the experiments. There were no detectable differences in the total predator densities in the *C. rodgersii* translocation experiment ($F_{5,48}$=0.9, p=0.41), the *H. rubra* tagging experiment ($F_{1,28}$=1.92, p=0.3), the experiment testing the effects of interspecific competition on *C. rodgersii* and *H. rubra* ($F_{2,28}$=0.38, p=0.68), or in the experiment testing the effects of intra- and interspecific competition on *H. rubra* ($F_{2,24}$=0.87, p=0.43). Similarly, there were no detectable differences among treatments in the densities of *Jasus edwardsii* or total fishes in the *C. rodgersii* translocation experiment ($F_{5,48}$=3.1, p=0.06 and $F_{5,48,}$=0.1, p=0.91, respectively), *H. rubra* tagging experiment ($F_{1,28}$=1.31, p=0.37 and $F_{1,28}$=0.15, p=0.71), experiment testing the effects of interspecific competition on *C. rodgersii* and *H. rubra* ($F_{2,\ 28}$=0.82, p=0.45 and $F_{2,28}$=0.08, p=0.93), or in the experiment testing the effects of intraspecific and interspecific competition on *H. rubra* ($F_{2,24}$=2.9, p=0.08 and $F_{2,24}$=0.9, p=0.42 respectively).

DISCUSSION

Climate change has the potential to alter competitive interactions between non-indigenous and native species (Walter et al. 2002 Firth et al. 2009). We examined competitive interactions between the non-indigenous urchin *Centrostephanus rodgersii* and the commercially fished abalone *Haliotis rubra.* Previous studies have examined interactions between these 2 herbivores (Shepherd 1973, Andrew et al. 1998, Strain & Johnson 2009, Chapter 3), but this is the first field study to experimentally test the effects of interspecific competition on *C. rodgersii* and *H. rubra* behaviour, movement and local abundances, in intact algal beds. There was strong evidence for asymmetrical interspecific competitive interactions between *C. rodgersii* and *H. rubra,* prior to any destructive grazing by the urchin.

Effects of interspecific competition on *C. rodgersii*

We tested the role of interspecific competition in explaining the establishment of *C. rodgersii* on the east coast of Tasmania. There was clear evidence of interspecific competition, but the nature of the interaction was asymmetrical. *C. rodgersii* negatively affects the behaviour, movement and local abundances of *H. rubra,* but there was no discernable effect of abalone on urchins. We found no detectable effects of the tagging and translocation

procedures on the resightability of the urchin. Assuming that abalone do not negatively affect juvenile urchins, which are largely cryptic and restricted to deeper crevices in the reef (Johnson et al. 2005), we find no evidence to suggest that removal of *H. rubra* through intensive fishing will influence the establishment and/or activity of *C. rodgersii.* In contrast, both intra- and interspecific competition negatively impacted on *H. rubra* behaviour transitions and movement patterns.

Effects of intra- and interspecific competition on *H. rubra*

Intra- and interspecific competition negatively impacted on *H. rubra* behavioural transitions. Abalone can move into the open to feed on drift algae and graze on the substratum however, some individuals feed on drift algae in cryptic shelter. In the control plots 75% of *H. rubra* remained exposed. However when *C. rodgersii* or extra abalone were added to plots, this proportion was halved, within 1 week of the experimental manipulations. Research in aquaculture tanks demonstrated that juvenile and adult abalone, stocked in at high densities spent less time out in the open feeding resulting in declines in individual total wet weight relative to controls with lower densities of abalone (Momma 1980, Huchette et al. 2003). This research suggests intra- and interspecific competition will negatively impact on *H. rubra* feeding behaviour, which could resulted in declines in growth in the wild.

Additions of *C. rodgersii* and extra abalone negatively impacted on *H. rubra* movement patterns. Abalone can be largely sedentary during the day (Shepherd 1973) when they occupy particular homescars or remain in cryptic shelter (Momma & Sato 1969, Shepherd 1973), and this behaviour was reflected in the high proportion of homing *H. rubra* (individuals that moved <0.4 m) in control plots. An increase in the density of competitors resulted in an increase in the both the proportion of mobile abalone (individuals that moved distances ≥0.4 m) and the mean net distance moved by abalone, within 1 week of the experimental manipulations. These changes in *H .rubra* movement patterns are likely to result in an increased risk of predation and a decreased time spent feeding (Momma & Sato 1969, Shepherd 1973, Branch 1975, Byers 2000b).

Relative effects of intra and interspecific competition on *H. rubra*

The experimental design allowed us to separate the relative effects of intra- and interspecific competition on *H. rubra*. Their relative strengths are critical

in assessing whether the climate induced range expansion of non-indigenous species will affect the distribution and abundance of native species (Byers 2000b, Firth et al. 2009). If intraspecific competition is stronger than interspecific competition, then coexistence can occur, but if the converse is true, the inferior competitor may be excluded (Bohn & Amundsen 2001, Byers 2000a).

The relative magnitude of intra- and interspecific competition on *H. rubra* differed depending on which response variable was considered. We found the effects of intra- and interspecific competition on *H. rubra* movement patterns were similar. In contrast, inter- rather than intraspecific competition had a stronger and more consistent impact on *H. rubra* behaviour transitions and resightability. These results suggest inter- rather than intraspecific competition is likely to have a stronger effect on *H. rubra*.

The negative impacts of *C. rodgersii* on *H. rubra* could be linked to interference competition for resources or to the presence of the urchin (Shepherd 1973, Andrew & Underwood 1992, Andrew et al. 1998, Strain & Johnson 2009, Chapter 3). Although not measured quantitatively, we frequently observed *C. rodgersii* and *H. rubra* juxtaposed, but with the abalone more cryptic than the urchin (Strain pers. obs., Worthington pers. comm.). *C. rodgersii* was often positioned at the opening of a rock or crevice while an adjacent *H. rubra* were positioned underneath a rock or at the back of a crevice. This behaviour could have limited abalone access to food or preferred habitat. Previous research has demonstrated abalone move in response to shortages of algae (Shepherd 1973) and homescars (Tarr et al. 1995). Our study suggests the introduction of *C. rodgersii* to plots could limit the availability of resources, resulting in *H. rubra* changing their behaviour, moving to new areas and declines in their resightability through time.

Effect of predators on *H. rubra*

We monitored the density and identity of predators in the various treatments. There were no detectable differences between treatments and no seasonal or site differences in the number of total predators (consisting of *Jasus edwardsii* and fishes) in the vicinity of plots. Only a small number of *H. rubra* were found dead, despite extensive searching of the site at the conclusion of the experiments. We find no evidence to suggest that

introducing extra abalone or *C. rodgersii* to plots, alters *H. rubra* risk of predation.

Impacts of *C. rodgersii* on *H. rubra* fisheries

The climate induced range expansion of *C. rodgersii* will negatively impact on the behaviour, movement and abundances of *H. rubra,* on the east coast of Tasmania. We demonstrated that the inclusion of *C. rodgersii* into intact algal beds causes *H. rubra* to seek shelter in cryptic habitat and flee, resulting in declines in their local abundances. The effects of *C. rodgersii* on *H. rubra* were consistent between seasons and through time. There were no detectable effects of the tagging procedure on *H. rubra.* These kinds of shifts in *H. rubra* behavior and movement will reduce the likelihood of abalone detection by fishers. We speculate that abalone growth will also be reduced because in the presence of the urchin, *H. rubra* will spend more time in cryptic habitat without readily available food. Previous research demonstrates that, the establishment of *C. rodgersii* at a site, will negatively impact on the body condition and survival of *H. rubra*. Clearly the continued expansion of *C. rodgersii* into Tasmania will negatively affect the abalone fishery productivity, prior to any destructive grazing.

Conclusions

Experimental research into the nature and effects of interactions between global climate induced range expanding non-indigenous species and native species is rare (Smith 2005, Firth et al. 2009, Ling 2009). Our study revealed the range expansion of key habitat modifying species is likely to have major negative impacts on valuable commercially fished native, through competition. The framework we proposed which included field-based experimental manipulations and Marklov chain modelling, may be widely applicable to the difficult task of predicting the impacts of other range expanding species on native species behaviour, movement, and local abundances. These results are important for predicting and managing the impacts of climate induced range expansions on commercially fished native species.

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CHAPTER 3: COMPETITION BETWEEN AN INVASIVE URCHIN AND COMMERCIALLY FISHED ABALONE: EFFECT ON BODY CONDITION, REPRODUCTION AND SURVIVORSHIP

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ABSTRACT

Incursion of the urchin *Centrostephanus rodgersii* into Tasmania, Australia, and its establishment at high densities raises questions about its potential interactions with another large herbivore on subtidal rocky reefs, the commercially fished abalone *Haliotis rubra*. Surveys on the southeast coast of Australia show a negative relationship between densities of *C. rodgersii* and *H. rubra* at several spatial scales, suggesting negative interactions. In intact algal beds, we used enclosures to estimate the effects and relative magnitude of intra- and interspecific competition on the body condition, gonad development and survival of *C. rodgersii* and *H. rubra*. An increased density of conspecifics led to declines in the dry gonad weight of *C. rodgersii* and in the dry foot and stomach content weights of *H. rubra*. The effects of interspecific competition were asymmetrical. Manipulations of *H. rubra* densities had no detectable effect on *C. rodgersii*. In contrast, in enclosures with added *C. rodgersii*, *H. rubra* showed reduced total and dry weights of stomach contents and increased mortality relative to controls without urchins. The effects of *C. rodgersii* on *H. rubra* could be linked to differences in feeding habits and morphology. *C. rodgersii* is a generalist herbivore, which, even at low densities, reduced the cover and standing biomass of total, brown and red algae relative to controls without urchins. In contrast, *H. rubra* is a specialist herbivore, which, even at high densities, had little effect on the cover and standing biomass of algae relative to the effect of *C. rodgersii*. This study suggests that the invader *C. rodgersii* is the superior competitor in interactions with *H. rubra*, and that its presence, even at low densities, affects the abalone fishery.

Key words: Invasion, Fishing, Competition, *Centrostephanus rodgersii*, *Haliotis rubra*

INTRODUCTION

With invasions of marine ecosystems increasing worldwide, it is important to identify the mechanisms of successful invasions to better predict future invaders, and to provide insight into the dynamics of invaded systems (Carlton 1992). The nature of competitive interactions between non-indigenous and native species can be an important determinant of invasion success, and the establishment of many non-indigenous species has been linked to superior competitive ability (Carlton 1992).). However, some non-indigenous species only become invasive when their competitors are removed, through either natural or human disturbances (Baltz & Moyle 1993). While there is substantial evidence that interspecific competition for food and/or shelter can be a key factor in invasion success in terrestrial and freshwater ecosystems, relatively few examples exist for marine ecosystems (Baltz & Moyle 1993, Byers 2000, Jensen et al. 2002).

The long-spined urchin *Centrostephanus rodgersii* has undergone a southerly range expansion from New South Wales, being first discovered in mainland Tasmania in 1978 (Edgar 1997). *C. rodgersii* and the blacklip abalone *Haliotis rubra* co-occur in similar habitat, and share predators and some overlap in diet in intact algal beds. This urchin is well known for its ability to overgraze macroalgal beds, resulting in a shift to 'barrens' habitat (Johnson et al. 2005). *C. rodgersii* barrens are becoming more widespread along the east coast of Tasmania and do not support viable fisheries of *H. rubra*. Whereas much of the research on the impacts of *C. rodgersii* on *H. rubra* densities has focused on barrens habitat, the nature of interactions between these 2 herbivores in intact algal beds, before any commencement of destructive urchin grazing, is not well understood. Assessing the effects of interspecific competition between *C. rodgersii* and *H. rubra* in intact algal beds is important to understand the mechanism behind the successful establishment of this urchin and the eventual exclusion of the abalone.

Interactions between abalone and urchins are complex and differ substantially between ecosystems. In Japan, South Africa and California, some urchin and abalone abundances are positively correlated, because juvenile abalone shelter beneath the spine canopy of adult urchins (Day & Branch 2000, Rogers-Bennett & Hearse 2001). In contrast, in Southeast Australia and New Zealand, abundances of the urchins *Centrostephanus rodgersii* (Andrew & Underwood 1992, Johnson et al. 2005) and *Evechinus chloroticus* (Naylor & Gerring 2001), respectively, are usually negatively correlated with *Haliotis* spp. at a range of spatial scales. Hypotheses to

explain negative correlations between *C. rodgersii* and *H. rubra* include competition for food (Shepherd 1973) and shelter (Andrew et al. 1998), but neither idea has been critically tested. Despite this, several authors have suggested that competition for food is the dominant interaction between *C. rodgersii* and *H. rubra*, because urchins are generalist herbivores, while abalone are specialist herbivores (Andrew 1989, Shepherd 1973).

Separating the effects and estimating the relative magnitude of intra- and interspecific competition for food is important in assessing the effects of competition. If the interspecific effects are stronger than the intraspecific effects, the establishment of *Centrostephanus rodgersii* may have negative impacts on the abundance and distribution of *Haliotis rubra*, or fishing abalone could facilitate the establishment of the urchin. Intraspecific competition for food has been demonstrated among *C. rodgersii* in New South Wales (Blount 2004) and some *Haliotis* spp. in Victoria (Huchette et al. 2003), but the effects of interspecific competition for food between *C. rodgersii* and *H. rubra* have not been tested. We manipulated densities of *C. rodgersii* and *H. rubra* in enclosures to test the effects and relative magnitude of intra- and interspecific competition for food on their body condition, gonad development and survival.

MATERIALS AND METHODS

Site characteristics

The experiment was conducted on subtidal rocky reefs at North Bay (42.52°S, 147.47°E), on the east coast of Tasmania, Australia, between February and August 2006. This site is characterised by gently sloping substratum reaching a depth of 15 to 17 m, with moderate topographic relief. Using the classification system proposed by Edgar (1984), it is described as moderately sheltered. North Bay is exposed to south-easterly swells, which, although infrequent, can be large. Reefs support a variety of habitat from small urchin barren patches (dominated by *Centrostephanus rodgersii* and without foliose algae) to areas dominated by diverse stands of canopy-forming algae, with a well-developed understorey.

The abundance, distribution and mean size of *Centrostephanus rodgersii* and *Haliotis rubra* were estimated from twenty 3x3 m quadrats positioned at a depth of between 3 and 17 m. The mean abundance and size of *C. rodgersii* was 10 individuals per 9 m^2 (+/-2 SE); the mean test diameter was 107.6 mm (+/-8.1 mm SE). The mean abundance and size of *H. rubra* was 10

individuals per 9 m^2 (+/-5 SE); the mean shell length was 119.67 mm (+/-3.3 mm SE). Animals were measured using vernier callipers.

Experimental design

We manipulated densities of *Centrostephanus rodgersii* and *Haliotis rubra* in enclosures to assess the effects and relative magnitude of intra- and interspecific competition at different densities. Enclosures were of nylon netting (3x3x1.5 m), with a mesh size of 50 mm, and were fully enclosed. Two rows of chain lined the bottom of the mesh, securing it to the bottom and preventing animal immigration and emigration. Enclosures were placed haphazardly ~10 m apart at depths of 10 to 12 m on intact algal reef where *C. rodgersii* and *H. rubra* co-occurred. All pre-existing *C. rodgersii* and *H. rubra* were removed. Initial assessments of the cover of different substratum types (large boulders >1 to <2.5 m diameter, mean +/-SE=26.11 +/-3.86%; small boulders >0.2 to <1 m diameter, mean +/-SE=66.85 +/-4.48%; and sand, mean +/-SE=7.04 +/-1.29%), cover of algal divisions (brown, green and red algae, mean +/-SE=75.93 +/-2.07, 14.08 +/-0.94 and 2.22 +/-0.79%, respectively) and density or cover of benthic invertebrates (urchins, mean +/-SE=0.56 +/-0.24% per 9 m^2; gastropods, mean +/-SE=1.82 +/-1.79% per 9 m^2; and sessile invertebrates, mean +/-SE=2.78 +/-3.76%) were made by eye.

Tagging *Centrostephanus rodgersii* and *Haliotis rubra*

C. rodgersii and *H. rubra* were collected from North Bay and tagged on the diving vessel. Abalone shells were scrubbed with a copper-wire bush, and hall print FPN (flexible polyethylene) tags (8x4 mm) were glued to the shell using Loctite 454. Urchins were tagged using a modification of the methods by Pederson & Johnson (2006). Two holes were made in the test using a 1.25 mm diameter hypodermic needle. The needle passed through the test between the oral and aboral surface. Monofilament fishing line (0.5 mm diameter) was threaded through the needle, which was then removed. Colour-coded beads were threaded over the line in individual combinations, which was closed as a loop with a number 4 size leader sleeve. Tagged *C. rodgersii* (test diameters from 104 to 116 mm and a measurement error mean +/-SE=1.89 +/-0.04 mm) and *H. rubra* (shell lengths from 114 to 126 mm) were allocated randomly to enclosures. Animals that died within 24 h after initiating treatments were replaced (3.92% abalone, 10.1% urchin).

Treatments

Treatments enabling tests of intraspecific competition (Tables 1 & 2) were 1x and 2x the ambient density of *Centrostephanus rodgersii* (1U0A vs. 2U0A) and *Haliotis rubra* (0U1A vs. 0U2A). Treatments enabling comparisons of interspecific competition (Tables 1 & 2) were 1x the ambient density of *C. rodgersii* with 1x the ambient density of *H. rubra* (1U1A), 1x the ambient density of *C. rodgersii* with 2x the ambient density of *H. rubra* (1U2A), 2x the ambient density *C. rodgersii* with 1x the ambient density of *H. rubra* (2U1A), and 2x the ambient density of *C. rodgersii* with 2x the ambient density of *H. rubra* (2U2A); 1x the ambient (average density at North Bay) and 2x the ambient (the maximum density at North Bay) densities of *H. rubra* and *C. rodgersii* were 10 and 20 individuals per 9 m^2, respectively. Enclosures were checked monthly and cleaned of accumulated algae and sediment. The identity of living *C. rodgersii* and *H. rubra* were recorded, and dead animals were removed. To test for the effect of enclosures on *C. rodgersii* and *H. rubra*, tagged animals were placed outside enclosures (n=3), at 1x the ambient density (1U0A and 0U1A). All pre-existing *C. rodgersii* and *H. rubra* were removed from control areas. Urchins and abalone did not reinvade these areas. The experiment was maintained for 6 months, at which time all animals were collected.

Table 1. *Centrostephanus rodgersii, Haliotis rubra.* Treatments involving manipulations of *C. rodgersii* (U) and *H. rubra* (A) densities in 9 m^2 enclosures. Ambient densities of *C. rodgersii* (1U0A) and *H. rubra* (0U1A) were 10 animals per 9 m^2. All treatments were multiples of these densities.

Treatments	1 1U0A	2 2U0A	3 1U1A	4 1U2A	5 2U1A	6 2U2A	7 0U1A	8 0U2A
C. rodgersii	10	20	10	10	20	20	0	0
H. rubra	0	0	10	20	10	20	10	20
H. rubra + *C. rodgersii*	10	20	20	30	30	40	10	20

Table 2. *Centrostephanus rodgersii*, *Haliotis rubra.* Details of comparisons to test for intra- and interspecific competition on *C. rodgersii* (U) and *H. rubra* (A), and effects of species on the cover and standing biomass of algae. Ambient densities of *C. rodgersii* (1U0A) and *H. rubra* (0U1A) were 10 animals per 9 m^2. All treatments were multiples of these densities. For the interspecific competition contrasts, treatments were pooled and linear coefficients recalculated.

Intra- vs. interspecific	Intraspecific	Effect of A and U densities	Cover, standing biomass algae
2U0A vs. 1U1A:effect of 2U relative to 1A 1U2A vs. 2U1A:effect of 1A relative to 2A	1U0A vs. 2U0A:effect of 2U	1U0A,2U0A vs. 1U1A,2U1A:effect of 1A 1U0A,2U0A vs. 1U2A,2U2A:effect of 2A 1U1A,2U1A vs. 1U2A,2U2A:effect of 1A relative to 2A	0U1A,0U2A vs. 1U0A,1U1A,1U2A:effect of 1U 0U1A,0U2A vs. 2U0A,2U1A,2U2A:effect of 2U 1U0A,1U1A,1U2A vs. 2U0A,2U1A,2U2A:effect of 1U relative to 2U
0U2A vs. 1U1A:effect of 2A relative to 1U 1U12A vs. 2U1A:effect of 1U relative to 2U	0U1A vs. 0U2A:effect of 2A	0U1A,0U2A vs. 1U1A,1U2A:effect of 1U 0U1A,0U2A vs. 2U1A,2U2A:effect of 2U 1U1A,1U2A vs. 2U1A,2U2A:effect of 1U relative to 2U	1U0A,2U0A vs. 0U1A,1U1A,2U1A:effect of 1A 1U0A,2U0A vs. 0U2A,1U2A,2U2A:effect of 2A 0U1A,1U1A,2U1A vs. 0U2A,1U2A, 2U2A:effect of 1A relative to 2A

Response variables

To assess body size increments, animals were returned to the laboratory and re-measured using vernier callipers, and these values were compared with initial measurements. Total wet weight was then recorded for each animal.

Animals were sexed, and their gonad development was assessed. To induce spawning in *Centrostephanus rodgersii*, specimens were injected with 5 ml of 0.05 μmol KCl, and spawn (presence, absence) and sex (males, female) were recorded. *C. rodgersii* were dissected, and their major body components (gonad, lantern, test and spines and stomach contents) were separated and dried for 3 days at 60°C before weighing.

Haliotis rubra were dissected, and their maturity (mature, immature) and sex (male, female) were determined by visual inspection of the gonad. If the testis or ovary could be discerned, they were considered to be sexually mature. The maturity and sex of abalone that were infected with trematode cercariae (6%) could not be determined, and those animals were excluded from this component of the analysis. Major body components of *H. rubra* (gonad, foot, shell, stomach contents) were separated, dried and weighed.

To determine the effects of *Centrostephanus rodgersii* and *Haliotis rubra* grazing on the abundance of attached algae in enclosures, the percentage cover of algal divisions (brown, red) was estimated by eye *in situ* at the conclusion of the experiment. A similar assessment was also made in the control areas. All algae were then collected by hand, bagged, returned to the laboratory and dried for 3 days at 60°C before weighing. Throughout the experiment, drift algae were also found both inside enclosures and in control areas, but because of high spatial and temporal variability in the abundance and condition of this resource, it was not collected.

Analysis

The effects of enclosures on increments (final–initial) of *Centrostephanus rodgersii* test width and *Haliotis rubra* shell length were analysed with 1-way ANOVA (main effect enclosures, fixed, 2 levels=present, absent). The effects of enclosures on the total wet weight and dry weights of body components of *C. rodgersii* and *H. rubra* were analysed with 1-way ANCOVA (main effect enclosures, fixed, 2 levels=present, absent, covariate=initial test width, shell length).

The impacts of enclosures on the gonad development of *Centrostephanus rodgersii* and *Haliotis rubra* (proportion of mature, spawning animals) were analysed using logistic modelling (see above details). In this analysis, generalized linear models were used, assuming a binomially distributed

response variable (maturity=mature, immature) using a logit function. Where significant differences were found, odds ratios and confidence intervals were calculated. We used the log-likelihood ratio test to assess the fit of the model.

The effects of intra- and interspecific competition on the increments of *Centrostephanus rodgersii* test width and *Haliotis rubra* shell length were analysed with 2-way ANOVA. To examine effects on *C. rodgersii*, the model included the main effects of urchins (fixed, 2 levels=1U, 2U), abalone (fixed, 3 levels=0A, 1A and 2A) and their interaction. Similarly, for *H. rubra*, the model included the main effects of abalone (fixed, 2 levels=1A, 2A) and *C. rodgersii* (fixed, 3 levels=0U, 1U and 2U), and their interaction.

The effects of intra- and interspecific competition on *Centrostephanus rodgersii* and *Haliotis rubra* weights were analysed with 2-way ANCOVA. The models included the main effects of urchin, abalone, the covariate and their interactions (see above details). To examine the effects on urchin and abalone dry gonad weight the models also included the main effect of sex (fixed, 2 levels=male, female).

The effects of intra- and interspecific competition on *Centrostephanus rodgersii* and *Haliotis rubra* gonad development were analysed using logistic modelling. Models included the main effects of *C. rodgersii*, *H. rubra*, the covariate and their interactions (see above details).

The effects of intra- and interspecific competition on *Centrostephanus rodgersii* and *Haliotis rubra* survivorship were analysed using the Cox proportional hazards regression model ('Survival' in R). For this analysis, animals whose remains could not be found and that did not die at the conclusion of the experiment were treated as censored observations. Models included the main effects of *C. rodgersii*, *H. rubra*, the covariate and their interactions (see above details). We used the Cox.zph function to test the proportional hazards assumption.

The effect of enclosures on the cover and standing biomass of the algal divisions was analysed with 1-way ANOVA (main effect enclosures, fixed, 2 levels=present, absent). The effect of *Centrostephanus rodgersii* and *Haliotis rubra* in the different treatments on the cover and biomass of the algal

divisions was analysed with an incomplete 2-way ANOVA. The model included the main effects of species (fixed, 2 levels=*C. rodgersii*, *H. rubra*) and density (fixed, 3 levels=0U, 1U, 2U and 0A, 1A, 2A), and their interaction.

Throughout the present study, ANCOVA was used to adjust for initial body size. For all parametric analyses, the relationship between standard deviation and means of treatment groups was used to determine the appropriate transformation to stabilise variances, and transformed data were checked for both normality (using normal probability plots) and homoscedasticity. For ANCOVAs, we also tested for homogeneity of slopes as the interaction between the covariate and the main effects. Where homogeneity of slopes was indicated, we presented the reduced models. Transformations are expressed in terms of the raw dependent variable, *Y*. Where significant differences were evident in the overall tests, planned comparisons between treatments were made (see Tables 1 & 2). Where comparison sets were non-orthogonal, the significance level was adjusted using the method by Todd & Keough (1994). All statistical analysis and graphics were undertaken using R.

RESULTS

Effect of enclosures on growth and gonad development

Very few tagged *Centrostephanus rodgersii* (n=8) and *Haliotis rubra* (n=6) were recovered from outside the enclosures and so these animals were pooled for analysis using unbalanced *t*-tests. There were no detectable effects of enclosures on increments of *C. rodgersii* test width (p=0.9), total weight (p=0.79), or dry weights of gonad (p=0.51), lantern (p=0.58), stomach contents (p=0.78), or spines and test (p=0.57). Similarly, there was no detectable effect of enclosures on increments of *H. rubra* shell length (p=0.3), total weight (p=0.75), or dry weights of gonad (p=0.5), foot (p=0.78), shell (p=0.6), or stomach contents (p=0.77). To check whether growth responses were independent of size, the body size increments of *C. rodgersii* and *H. rubra* were plotted against their total weight and dry body component weights. No significant relationships were evident.

The effect of enclosures on the gonad development of *Centrostephanus rodgersii* and *Haliotis rubra* were analysed with a row × column test of independence, using *G*-tests. To compensate for increased Type I error and low numbers, William's correction (*q*) was used. There were no detectable

effects of enclosures on the proportion of *C. rodgersii* that spawned (p=0.88) or the proportion of mature *H. rubra* (p=0.72).

Effect of competition on body size increments

There was no evidence that intra- and interspecific competition affected increments in *Centrostephanus rodgersii* test width (*C. rodgersii*, $F_{1,155}$=0.1, p=0.93; *Haliotis rubra*, $F_{2,155}$=0.61, p=0.26; *C. rodgersii* x *H. rubra*, $F_{2,155}$=0.18, p=0.84) or increments in *H. rubra* shell length (*H. rubra*, $F_{1,155}$=1.32, p=0.9; *C. rodgersii*, $F_{2,155}$=0.08, p=0.99; *C. rodgersii* x *H. rubra*, $F_{2,155}$=1.21, p=0.12).

Effect of competition on total body and body component weights

There were significant effects of intra- and interspecific competition on *Centrostephanus rodgersii* and *Haliotis rubra* (Figures 1, 2, Table 3). The nature of the effects and relative magnitude of intra- and interspecific competition on *C. rodgersii* and *H. rubra* varied according to the body components measured.

Increases in the density of conspecifics negatively influenced the body component weights of *Centrostephanus rodgersii* and *Haliotis rubra.* Average dry gonad weight was reduced by 40% when densities of *C. rodgersii* doubled. However, manipulations of *C. rodgersii* densities had no detectable effects on total wet weight or dry weights of lanterns, stomach contents, or test and spines. For *H. rubra,* increases in the density of conspecifics led to reduced dry weights of foot and stomach contents. When densities of *H. rubra* were doubled, average dry foot weight was reduced by 8%, and the dry weight of stomach contents was reduced by 22.6%. However, manipulations of abalone densities had no detectable effects on *H. rubra* total weight or the dry weights of gonad and shell.

Manipulations of *Haliotis rubra* densities had no detectable effects on *Centrostephanus rodgersii* total weight or the dry weights of urchin gonad, lantern, stomach contents, or test and spines. In contrast, inclusion of *C. rodgersii* in the enclosures at both ambient and double ambient densities resulted in significant but similar reductions in *H. rubra* total weight and dry weights of stomach contents relative to controls without urchins. The effects of *C. rodgersii* on dry gonad weight of *H. rubra* were only significant at double ambient densities when compared to controls without urchins. There

were no detectable effects of *C. rodgersii* on the dry shell weight of *H. rubra.*

There were no detectable differences in the relative effects of intra- and interspecific competition on the dry weights of *Haliotis rubra* gonad and foot. In contrast, inter- rather than intraspecific competition accounted for declines in *H. rubra* total weight and in the weight of dry stomach contents.

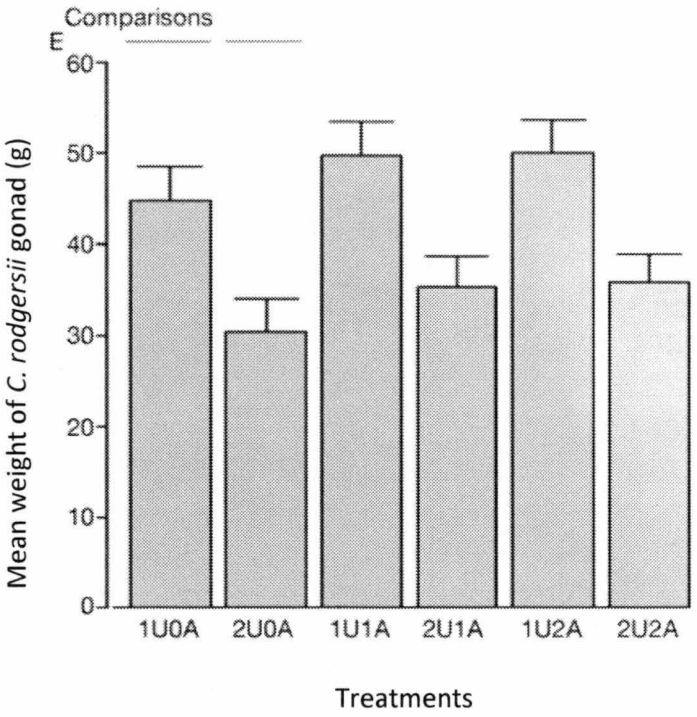

Figure 1. *Centrostephanus rodgersii* and *Haliotis rubra.* Effects of intra- and interspecific competition on mean gonad dry weight (g) (see Table 3). Data are means (+/-SE) of n=3. 1U and 2U: 1x and 2x ambient density *C. rodgersii;* 0A, 1A and 2A: 0x, 1x and 2x ambient density *H. rubra.* Comparison is E: 1U0A vs. 2U0A. Single lines above indicate significant differences between treatment means.

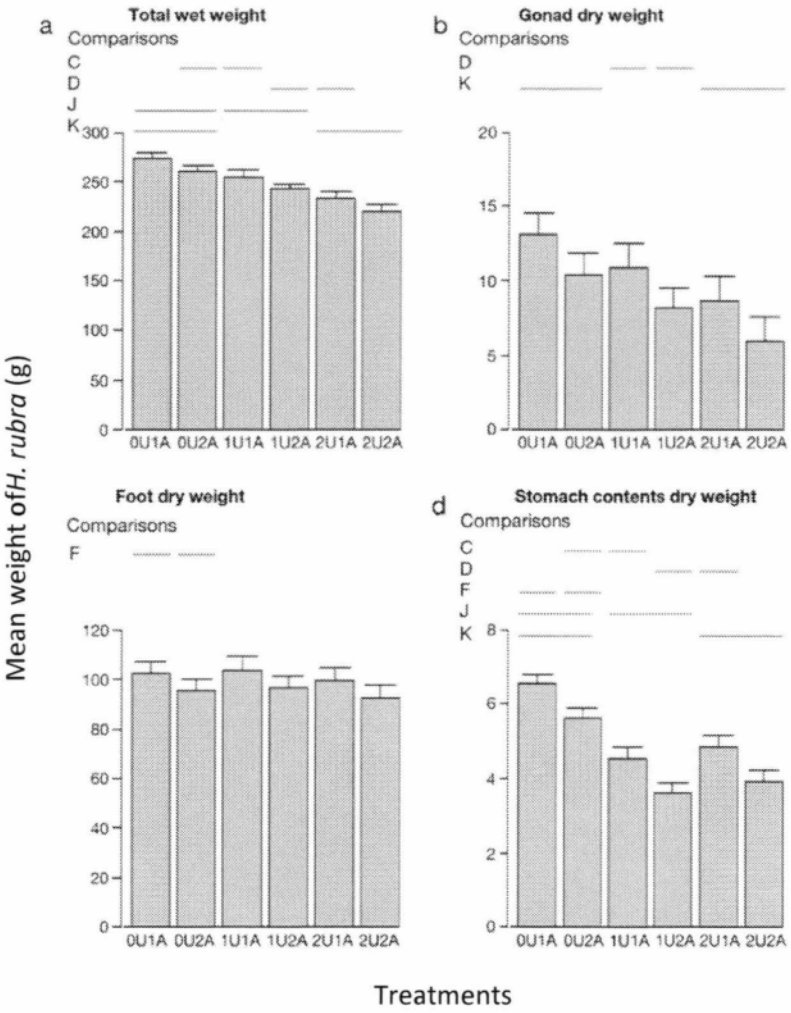

Figure 2. *Centrostephanus rodgersii*, *Haliotis rubra.* Effects of intra- and interspecific competition on mean (a) total wet weight, and dry weights (g) of (b) gonad, (c) foot and (d) stomach content (see Table 3). Data are means (+/-SE) of n=3. 0U, 1U and 2U: 0x, 1x and 2x ambient density *C. rodgersii*; 1A and 2A: 1x and 2x ambient density *H. rubra.* Comparisons are— C: 0U1A vs. 0U2A; D: 1U2A vs. 2U1A; F: 0U1A vs. 0U2A; J: 0U1A, 0U2A vs. 1U1A, 1U2A; K: 0U1A, 0U2A vs. 2U1A, 2U2A. Single lines above indicate significant differences between treatment means, and connecting lines indicate significant differences between groups of treatment means.

Table 3. *Centrostephanus rodgersii*, *Haliotis rubra.* Results of ANCOVA testing effects of intra- and interspecific competition on growth of *C. rodgersii* and *H. rubra* expressed as total wet body weight and dry weight of body components (g). Significant p-values are in bold print: $p<0.05$ values are significant for the main analysis and $p<0.01$ values are significant for comparisons (α-adjusted using Todd & Keough (1994)).

Source of variation	df	MS	*F*	p	Comparisons	*F*	p	Effect size
C. rodgersii								
Total wet weight [log(y + 0.001)]								
Urchin	1	0.01	0.28	0.59				
Abalone	2	0.17	4.88	0.1				
Urchin x Abalone	2	0.04	1	0.38				
Initial test width	1	2.49	71.29	**1^{e-14}**				
Residual	159							
Gonad dry weight								
Urchin	1	7439	15.45	**1^{e-4}**	1U0A vs. 2U0A	13.213	**1^{e-4}**	–20.81
Abalone	2	803	1.67	0.2				
Urchin x Abalone	2	1011	2.1	0.13				
Sex	1	1092	2.59	0.11				
Initial test width	1	2563	5.32	**0.02**				
Residual	125	1011						
Lantern dry weight [log (y + 0.0001)]								
Urchin	1	0.05	0.09	0.09				
Abalone	2	0.01	0.47	0.63				
Urchin x Abalone	2	0.01	0.17	0.85				
Initial test width	1	0.74	53.4	**1^{e-11}**				
Residual	159	0.02						

Stomach content dry weight [log(y + 0.001)]								
Urchin	1	0.09	0.66	0.42				
Abalone	2	0.06	0.34	0.72				
Urchin x Abalone	2	0.12	1.14	0.33				
Initial test width	1	0.11	1.8	0.18				
Residual	159							
Test and spines dry weight								
Urchin	1	0.14	0.7	0.4				
Abalone	2	0.08	1.31	0.28				
Urchin x Abalone	2	0.21	1.15	0.32				
Initial test width	1	0.28	98.28	**2^{e-16}**				
Residual	159	0.21						
H. rubra								
Total wet weight [log(y + 0.001)]					0U2A vs. 1U1A	10.86	**0.01**	–17.33
Urchin	2	16090	20.22	**6^{e-8}**	1U2A vs. 2U1A	10.11	**0.01**	–16.9
Abalone	1	805	1.01	0.32	0U1A,0U2A vs. 1U1A,1U2A	10.36	**2^{e-3}**	–20.97
Urchin × Abalone	2	2036	2.45	0.1	0U1A,0U2A vs. 2U1A,2U2A	30.42	**7^{e-7}**	–42.48
Initial shell length	1	1947	25.6	**3^{e-6}**	1U1A,1U2A vs. 2U1A,2U1A	4.42	0.03	–19.79
Residual	89	796						
Gonad dry weight [log(y + 0.0001)]					0U2A vs. 1U1A	4.71	0.04	–2.26
Urchin	2	0.83	13.61	**1^{e-5}**	1U2A vs. 2U1A	1.64	0.18	5.56
Abalone	1	0.02	0.3	0.6	0U1A vs. 0U2A	2.84	0.11	–8.3
Urchin x Abalone	2	0.29	4.82	**0.02**	0U1A,0U2A vs. 1U1A,1U2A	3.09	0.05	–3.9
Initial shell length	1	0.77	12.28	**7^{e-4}**	0U1A,0U2A vs. 2U1A,2U2A	18.33	**6^{e-5}**	–10.24
Sex	1	0.2	3.23	0.1	1U1A,1U2A vs. 2U1A,2U2A	7.14	**9^{e-3}**	–6.09
Residual	88	0.06						

Foot dry weight [sqrt(y)]					0U2A vs. 1U1A	1.44	0.24	–1.24
Urchin	2	1.17	0.92	0.35	1U2A vs. 2U1A	2.56	0.5	–4.53
Abalone	1	1.88	1.3	0.3	0U1A vs. 0U2A	15.55	$\mathbf{1^{e-3}}$	–18.67
Urchin x Abalone	2	7.34	6.1	**0.01**	0U1A,0U2A vs. 1U1A,1U2A	0.03	0.86	–2
Initial shell length	1	22.3	17.72	$\mathbf{6^{e-5}}$	0U1A,0U2A vs. 2U1A,2U2A	0.62	0.44	–5.98
Residual	89	1.27			1U1A,1U2A vs. 2U1A,2U2A	0.45	0.51	–3.32
Shell dry weight [log(y + 0.0001)]								
Urchin	2	292	0.65	0.52				
Abalone	1	35	0.08	0.79				
Urchin x Abalone	2	133	0.3	0.75				
Initial shell length (covariate)	1	1139	2.51	0.12				
Residual	85	454						
Stomach content dry weight [log(y + 0.001)]					0U2A vs. 1U1A	10.71	$\mathbf{3^{e-3}}$	–2.19
Urchin	2	1.87	32.75	$\mathbf{3^{e-11}}$	1U2A vs. 2U1A	8.07	$\mathbf{8^{e-3}}$	–1.37
Abalone	1	0.81	18.6	$\mathbf{2^{e-4}}$	0U1A vs. 0U2A	15.04	$\mathbf{4^{e-4}}$	–1.21
Urchin x Abalone	2	0.4	7.71	$\mathbf{1^{e-3}}$	0U1A,0U2A vs. 1U1A,1U2A	60.58	$\mathbf{7^{e-11}}$	–0.13
Initial shell length	1	0.4	5.47	**0.02**	0U1A,0U2A vs. 2U1A,2U2A	22.16	$\mathbf{2^{e-6}}$	–1.86
Residual	85	0.06			1U1A,1U2A vs. 2U1A,2U2A	1.83	0.21	–0.06

Effect of competition on gonad development

There was no evidence that either intra- or interspecific competition influenced the proportion of *Centrostephanus rodgersii* that spawned (*C. rodgersii*, Z=2.09, df=1, p=0.99; *Haliotis rubra*, Z=0.75, p=0.99; *C. rodgersii* x *H. rubra*, Z=1.49, df=2, p=0.14).

In contrast, inclusion of *Centrostephanus rodgersii* in enclosures at ambient or double ambient densities resulted in similar declines in the proportion of mature *Haliotis rubra* relative to controls without urchins (Figure 3, Table 4). Differences in the relative effects of intra- and interspecific competition were not significant.

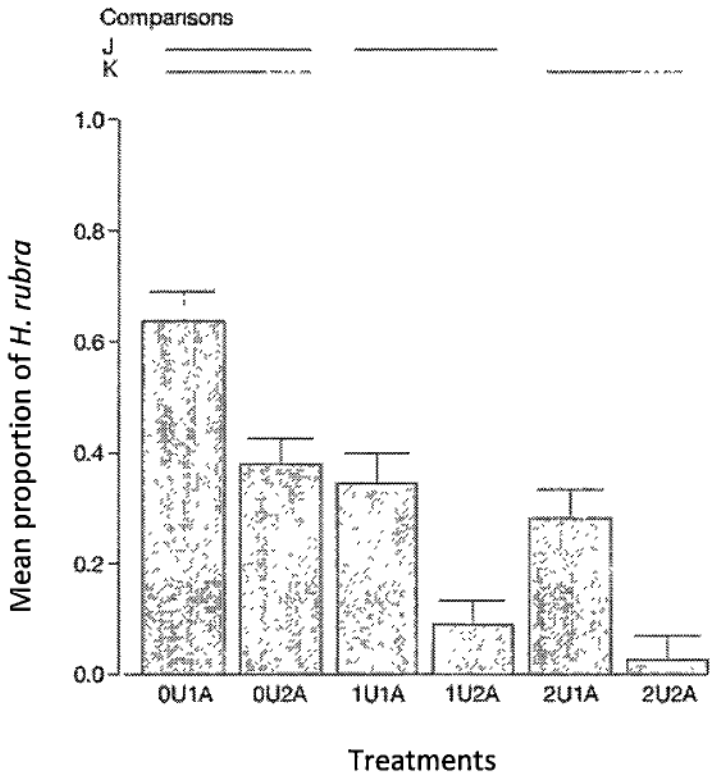

Figure 3. *Centrostephanus rodgersii*, *Haliotis rubra*. Effects of intra- and interspecific competition on the proportion of mature *H. rubra* (see Table 4) Data are means (+/-SE) of n=3. 0U, 1U and 2U: 0x, 1x and 2x ambient density *C. rodgersii*; 1A and 2A: 0x, 1x and 2x ambient density *H. rubra* Comparisons are— J: 0U1A, 0U2A vs. 1U1A, 1U2A; K: 0U1A, 0U2A vs. 2U1A, 2U2A. Connecting lines indicate significant differences between groups of treatment means.

Effect of competition on survivorship

There was some mortality of *Centrostephanus rodgersii* (36.4%) and *Haliotis rubra* (42.15%) during the experiment (Figures 4, 5, Table 4), but no evidence that intra- or interspecific competition affected survivorship of *C. rodgersii*. In contrast, manipulation of *C. rodgersii* densities suggests that the presence of the urchin at ambient densities leads to a decrease in the survivorship of *H. rubra*. However, the effects of *C. rodgersii* on *H. rubra* survivorship at ambient and double ambient densities were similar.

Table 4. *Centrostephanus rodgersii*, *Haliotis rubra*. Results of logistic regression and survival analysis testing effects of intra- and interspecific competition on *H. rubra* gonad development and *C. rodgersii* and *H. rubra* survivorship through time. Significant p-values are in bold print: $p < 0.05$ values are significant for the main analysis and $p < 0.01$ values are significant for comparisons (α-adjusted using Todd & Keough (1994)).

Source of variation	df	Deviance residual	Residual deviance	p	Comparisons	Residual deviance	p	Effect size
Logistic regression								
H. rubra								
Null			123.28		0U2A vs. 1U1A	31.46	0.03	–1.69
Urchin	1	15.28	106.72	**4^{e-5}**	1U2A vs. 2U1A	41.28	0.23	1.03
Abalone	2	1.29	122	0.26	0U1A vs. 0U2A	32.68	**2^{e-3}**	–2.7
Urchin x Abalone	2	15.49	106.72	**4^{e-5}**	0U1A,0U2A vs. 1U1A,1U2A	81.92	**5^{e-2}**	–1.34
Initial shell length	1	0	106.72	0.97	0U1A,0U2A vs. 2U1A,2U2A	66.12	**1^{e-3}**	–2.54
Survival analysis								
C. rodgersii								
Null			1174.65					

Urchin	1	2.09	1172.56	0.35				
Abalone	2	0.75	1171.81	0.39				
Urchin x Abalone	2	3.58	1168.23	0.17				
H. rubra					0U2A vs. 1U1A	256.24	0.1	–0.37
Null			1012.99		1U2A vs. 2U1A	556.24	**0.01**	–0.67
Urchin	2	11.24	1001.71	$\mathbf{3^{e-3}}$	0U1A, 0U2A vs. 1U1A,1U2A	545.88	**0.01**	–0.73
Abalone	1	4.65	1012.95	0.85	0U1A,0U2A vs. 2U1A,2U2A	579.32	$\mathbf{2^{e-3}}$	–0.82
Urchin x Abalone	2	0.03	997.06	0.1	1U1A,1U2A vs. 2U1A,2U1A	739.41	0.64	–0.11

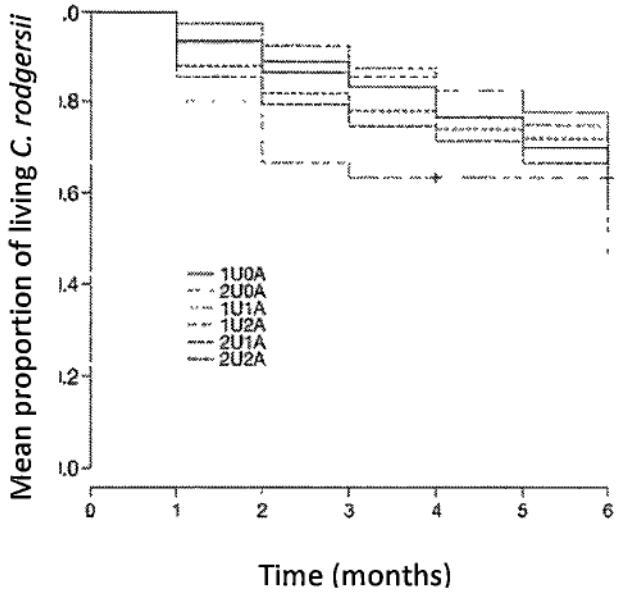

Figure 4. *Centrostephanus rodgersii*, *Haliotis rubra*. Effects of intra- and interspecific competition on the proportion of living individuals through time (see Table 4). Data are means (+/-SE) of n=3. 1U and 2U: 1x and 2x ambient density *C. rodgersii*; 0A, 1A and 2A: 0x, 1x and 2x ambient density *H. rubra*

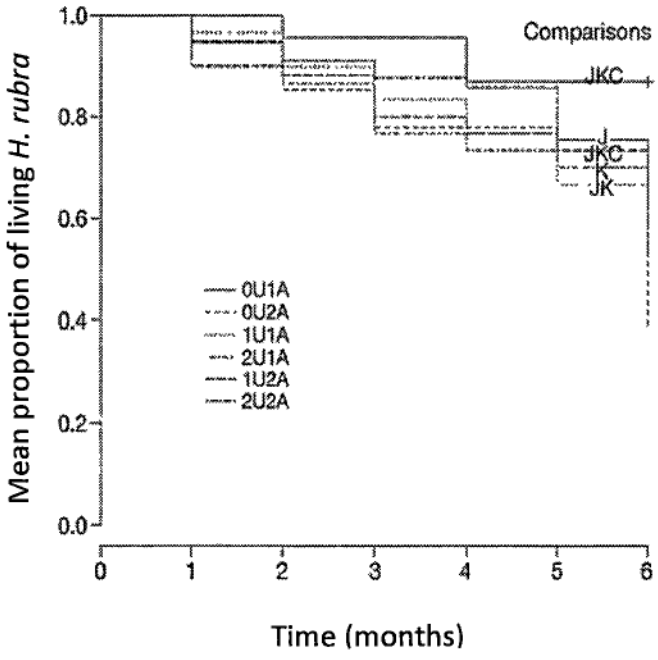

Figure 5. *Centrostephanus rodgersii*, *Haliotis rubra*. Effects of intra- and interspecific competition the proportion of living of *H. rubra* through time (see Table 4). Data are means (+/-SE) of n=3. 0U, 1U and 2U: 0x, 1x and 2x ambient density *C. rodgersii*; 1A and 2A: 1x and x ambient density *H. rubra*. Comparisons are— C: 0U2A vs. 1U1A; J: 0U1A, 0U2A vs. 1U1A, 2U1A; K: 0U1A, 0U2A vs. 2U1A, 2U2A. Letters indicate significant differences between treatment means and between groups of treatment means.

Effects of enclosures and grazing on algae

There were no significant effects of enclosures on the cover of total algae ($F_{1,4}$=0.46, p=0.88) or on brown ($F_{1,4}$=0.14, p=0.12) and red components of the algal assemblage ($F_{1,4}$=1, p=0.99). There were no significant effects either of enclosures on the biomass of total ($F_{1,4}$=0.01, p=0.23) or brown ($F_{1,4}$=1.05, p=0.34) and red ($F_{1,4}$=0.6, p=0.77) algae.

Grazing by *Haliotis rubra* over 6 months resulted in a slight but not significant decline in the standing biomass and cover of red algae. In contrast, additions of *Centrostephanus rodgersii* at ambient density or greater resulted in linear declines in the cover and standing biomass of total algae and of brown and red algae (Figures 6, 7, Table 5).

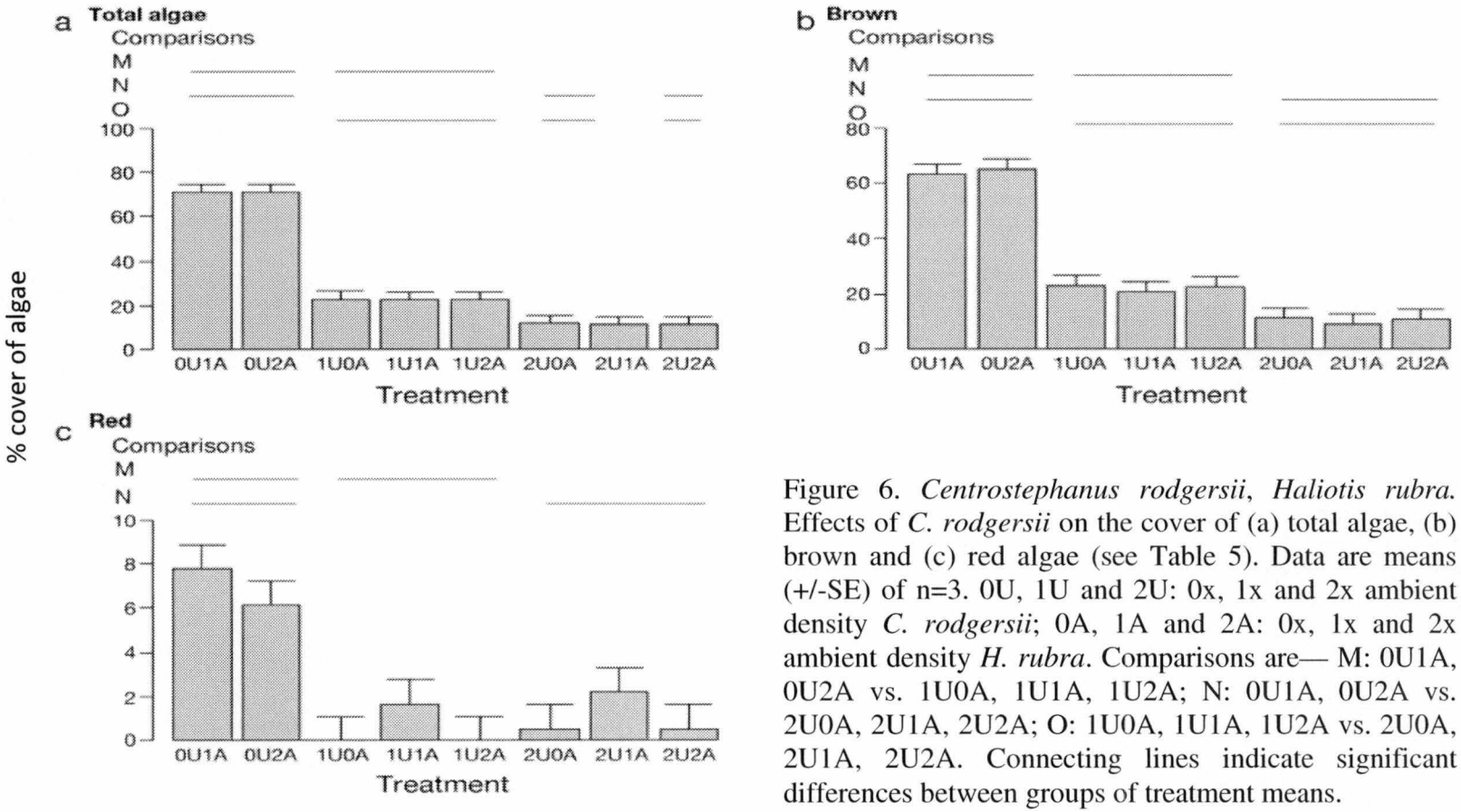

Figure 6. *Centrostephanus rodgersii*, *Haliotis rubra*. Effects of *C. rodgersii* on the cover of (a) total algae, (b) brown and (c) red algae (see Table 5). Data are means (+/-SE) of n=3. 0U, 1U and 2U: 0x, 1x and 2x ambient density *C. rodgersii*; 0A, 1A and 2A: 0x, 1x and 2x ambient density *H. rubra*. Comparisons are— M: 0U1A, 0U2A vs. 1U0A, 1U1A, 1U2A; N: 0U1A, 0U2A vs. 2U0A, 2U1A, 2U2A; O: 1U0A, 1U1A, 1U2A vs. 2U0A, 2U1A, 2U2A. Connecting lines indicate significant differences between groups of treatment means.

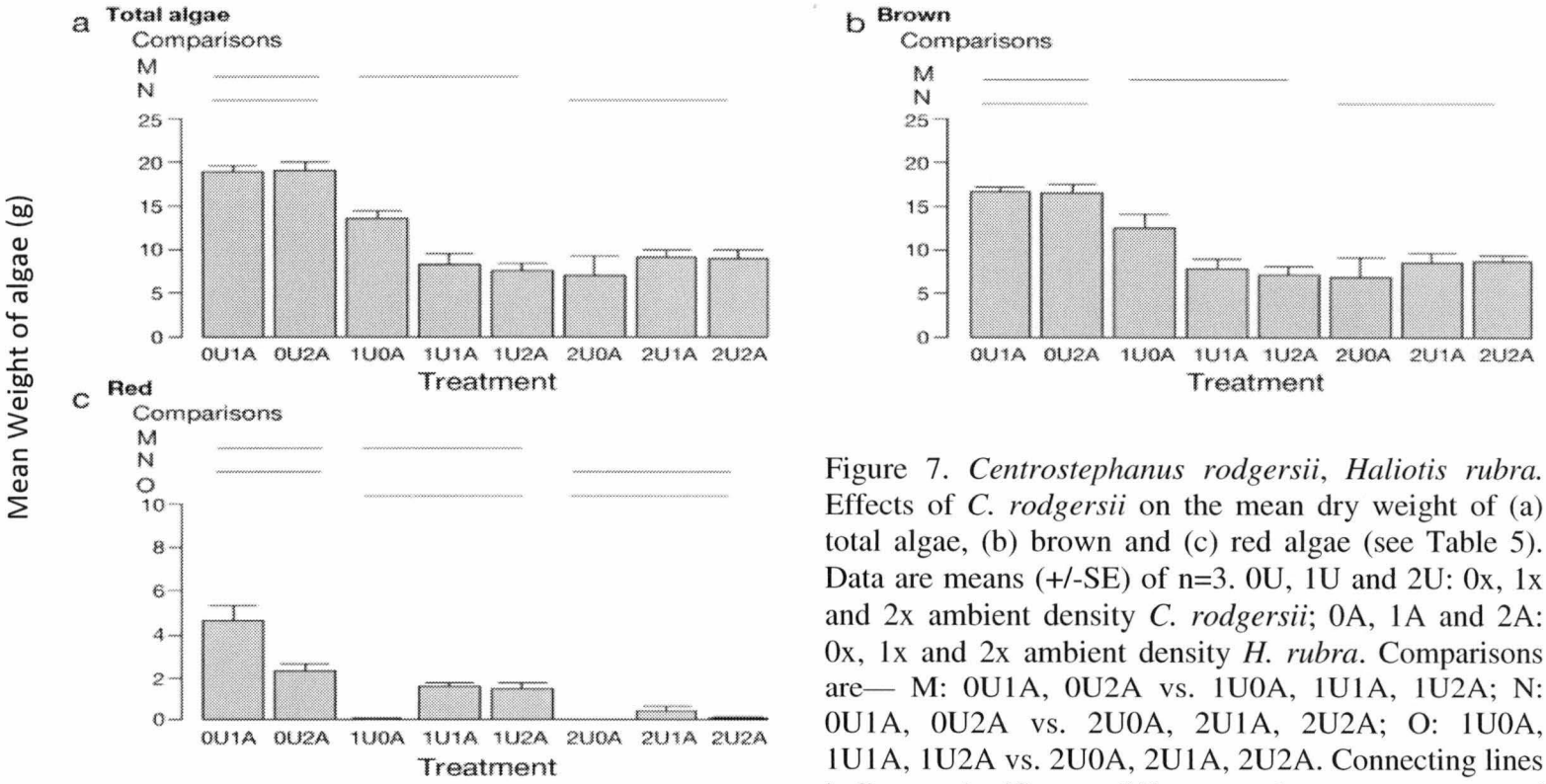

Figure 7. *Centrostephanus rodgersii*, *Haliotis rubra*. Effects of *C. rodgersii* on the mean dry weight of (a) total algae, (b) brown and (c) red algae (see Table 5). Data are means (+/-SE) of n=3. 0U, 1U and 2U: 0x, 1x and 2x ambient density *C. rodgersii*; 0A, 1A and 2A: 0x, 1x and 2x ambient density *H. rubra*. Comparisons are— M: 0U1A, 0U2A vs. 1U0A, 1U1A, 1U2A; N: 0U1A, 0U2A vs. 2U0A, 2U1A, 2U2A; O: 1U0A, 1U1A, 1U2A vs. 2U0A, 2U1A, 2U2A. Connecting lines indicate significant differences between groups of treatment means.

Table 5. *Centrostephanus rodgersii, Haliotis rubra.* Results of ANOVAs testing the effects of *C. rodgersii* and *H. rubra* on the cover and dry weight (g) of total algae, brown and red algae. Significant p-values are in bold print: $p<0.05$ values are significant for the main analysis and $p<0.016$ values are significant for comparisons (α-adjusted using Todd & Keough (1994)).

Source of variation	df	MS	*F*	p	Comparisons	*F*	p	Effect size
Cover								
Total algae								
Urchin	2	6947.2	92.63	**2^{e-9}**	0U1A,0U2A vs.1U0A,1U1A,1U2A	102.73	**2^{e-7}**	–49.72
Abalone	2	5.6	0.08	0.93	0U1A,0U2A vs.2U0A,2U1A,2U2A	190.73	**4^{e-9}**	–60.84
Urchin x Abalone	3	59.3	0.79	0.52	1U0A,1U1A,1U2A vs. 2U,2U1A,2U2A	11.04	**5^{e-3}**	–11.1
Residual	16	75.0						
Brown algae								
Urchin	2	5442.4	64.5	**2^{e-8}**	0U1A,0U2A vs. 1U0A,1U1A,1U2A	67.14	**2^{e-6}**	–42.78
Abalone	2	11.8	0.14	0.87	0U1A,0U2A vs. 2U0A,2U1A, 2U2A	142.63	**2^{e-8}**	–54.45
Urchin x Abalone	3	58.3	0.69	0.57	1U0A,1U1A,1U2A vs.2U,2U1A,2U2A	10.57	**5^{e-3}**	–11.68
Residual	16	84.4						
Red algae [log(y + 0.001)]								
Urchin	2	100.7	19.34	**5^{e-5}**	0U1A,0U2A vs. 1U0A,1U1A,1U2A	37.79	**3^{e-5}**	–7.92
Abalone	2	6.25	1.2	0.33	0U1A,0U2A vs. 2U0A,2U1A,2U2A	25.01	**3^{e-3}**	**–7**
Urchin x Abalone	3	0.93	0.18	0.91	1U0A,1U1A,1U2Avs.2UA,2U1A,2U2A	0.37	0.56	–.95
Residual	16	5.21						
Dry weight								
Total algae [sqrt(y)]					0U1A,0U2A vs. U0A,1U1A,1U2A	45.78	**6^{e-6}**	–1.28
Urchin	2	5.47	42.74	**3^{e-7}**	0U1A,0U2A vs. 2U0A,2U1A,2U2A	72.88	**3^{e-7}**	–1.51
Abalone	2	0.09	0.68	0.53	1U0A,1U1A,1U2A vs. A,2U1A,2U2A	1	0.35	–0.23
Urchin x Abalone	3	0.43	3.34	**0.04**	1U0A,2U0A vs. 0U1A,1U1A,1U2A	0.01	0.93	–0.04

Residual	16	0.13			1U0A,2U0A vs. 0U2A,1U2A,2U2A	0.04	0.86	–0.08
Brown algae [sqrt(y)]								
Urchin	2	4.31	31.1	$\mathbf{2^{e-6}}$	0U1A,0U2A vs. 1U0A,1U1A,1U2A	36.3	$\mathbf{2^{e-5}}$	–6.03
Abalone	2	0.14	1	0.4	0U1A, 0U2A vs. 2U0A,2U1A,2U2A	54.56	$\mathbf{2^{e-6}}$	–1.34
Urchin x Abalone	3	0.36	2.57	0.08	1U0A,1U1A,1U2A vs.2U,2U1A,2U2A	0.74	0.4	–0.2
Residual	16	0.14						
Red algae								
Urchin	2	8.84	18.51	$\mathbf{6^{e-5}}$	0U1A,0U2A vs. 1U0A,1U1A,1U2A	16.85	$\mathbf{1^{e-3}}$	–2.45
Abalone	2	0.07	0.14	0.88	0U1A,0U2A vs. 2U0A,2U1A,2U2A	43	$\mathbf{2^{e-5}}$	–3.34
Urchin x Abalone	3	0.21	0.44	0.78	1U0A,1U1A,1U2A vs.2U,2U1A,2U2A	9.6	$\mathbf{7^{e-3}}$	–0.88
Residual	16	0.48						

DISCUSSION

One of the crucial questions in invasion biology is to quantify the nature, direction and results of interspecific competitive interactions for food between invasive and native species (Byers 2000). We examined competitive interactions between the invasive urchin *Centrostephanus rodgersii* and the commercially fished abalone *Haliotis rubra*. Previous studies have examined interactions between these 2 herbivores (Shepherd 1973, Andrew et al. 1998), but the present work is the first field study to experimentally test the effect of competition for food on *C. rodgersii* and *H. rubra* body condition, gonad development and survival, in intact algal beds. There was strong evidence for intra- and interspecific competitive interactions for food between *C. rodgersii* and *H. rubra*, prior to any destructive grazing by the urchin.

Effects of intraspecific competition

Intraspecific competition for food had marked effects on the body condition of *Centrostephanus rodgersii* and *Haliotis rubra*. Doubling the ambient density of conspecifics led to declines in the dry gonad weight of *C. rodgersii*, and the dry foot and stomach content weights of *H. rubra* within the 6 month time frame of the experiment. Our results are likely to be representative of natural populations, because treatment densities were well within naturally occurring densities of *C. rodgersii* and *H. rubra* in Tasmania, and in some areas their densities can greatly exceed those tested (Johnson et al. 2005). Furthermore and notably, there was no evidence that the body condition and gonad development of either species was influenced by enclosures.

Our findings are consistent with other research results on the effect of intraspecific competition in urchins, including *Centrostephanus rodgersii* (Blount 2004). Individuals co-existing at high densities in barrens are often smaller (test width and height) and have smaller gonads (wet weight), than those at sites with fewer urchins (Bryne et al. 1998), and in individuals in intact algal beds (Ling et al. 2008). Blount (2004) found that, in barrens, *C. rodgersii* in low-density treatments (33 and 66% removals) had larger gonads relative to body size and increased growth (estimated from jaw pieces) and fecundity (number of eggs) compared to individuals in high-density treatments (0% removal). It seems clear that an increased density of urchins has deleterious effects on the body condition and reproductive output of individual *C. rodgersii* in the wild; however, the impacts are intensified in a barrens habitat compared with in intact algal beds (Ling et al. 2008).

Effects of interspecific competition

We tested the role of interspecific competition for food in explaining the establishment of *Centrostephanus rodgersii* and the eventual exclusion of *Haliotis rubra* from intact algal beds. There was clear evidence of interspecific competition, but the nature of the interaction was asymmetrical. *C. rodgersii* negatively affects the body condition and survival of *H. rubra*, but there was no discernable effect of abalone on urchins. These results suggest that removal of *H. rubra* through intensive fishing is unlikely to be important in facilitating the establishment of *C. rodgersii* on the east coast of Tasmania.

Our findings are similar to those of the only other published study on interspecific competition for food between urchins and abalone (Tegner & Levin 1982). Inclusion of *Strongylocentotus franciscanus* in tanks had a negative effect on the total weight of *Haliotis rufescens* relative to tanks without urchins. Contrary to our study, Tegner & Levin (1982) also demonstrated that *H. rufescens* had a negative impact on *S. franciscanus* test width and total weight. However, the importance of competition for food between these 2 herbivores in the wild is questionable, as there are substantial problems in extrapolating the results from tanks to the wild. Tegner & Levin (1982) also had only 1 replicate tank for all treatments, their animals were weighed monthly, and the high variability in weight could have been influenced by handling stress (Ragg et al. 2000). Further testing is required to ascertain the nature of effects of interspecific competition for food on the growth of *S. franciscanus* and *H. rufescens* in the wild.

Relative effects of intra- and interspecific competition

The design allowed us to separate the relative effects of intra- and interspecific competition. Their relative strengths are critical in assessing whether interspecific competition has an important impact on the distribution and abundance of native and invasive herbivores (Byers 2000). If intraspecific competition is stronger than interspecific competition, then coexistence can occur (Berman & Carlton 1991, Byers 2000), but, if the reverse situation exists, the inferior competitor may be excluded. The relative effects of competition differed between *Centrostephanus rodgersii* and *Haliotis rubra.*

Intra- but not interspecific competition resulted in declines in *Centrostephanus rodgersii* dry gonad weight. However, increases in urchin and abalone densities had no effect on *C. rodgersii* total weight, or the dry weight of the lantern, stomach contents, or test and spines combined, or the proportion of individuals that spawned or survived. This differential could be explained by the adaptations of urchins to food limitations. An increase in urchin density results in declines in the availability of preferred and total food, which could lead to an increase in food processing times and result in declines in dry gonad weight (Tenger & Dayton 1982, Andrew 1989). Overall the evidence suggests that neither intra- nor interspecific competition has an important influence on *C. rodgersii* abundances in intact algal beds within the 6 mo time frame of our experiment. Further evidence comes from Ling et al. (2008), who demonstrated that high urchin densities had very little

impact on *C. rodgersii* reproductive capacity or total weight in intact algal beds.

For *Haliotis rubra*, the relative effects of intra- and interspecific competition varied depending on the response variables measured. The effects of intra- and interspecific competition on the dry weights of gonad and foot and on the proportion of mature abalone were similar. In contrast, inter- but not intraspecific competition led to declines in *H. rubra* in total weight, dry weight of stomach contents and survival of abalone. These results could be explained by the differences in *H. rubra* and *C. rodgersii* feeding preferences. An increase in abalone densities resulted in declines in the availability of preferred food and declines in *H. rubra* reproductive capacity, while the addition of *C. rodgersii* to the system reduces the total availability of food, with negative effects on abalone body condition and survival. These results suggest that inter- rather than intraspecific competition is likely to have stronger effects on *H. rubra.*

Effects on algae

For competition to affect the abundance and distribution of species, a common resource must be limiting (Byers 2000). *Centrostephanus rodgersii* and *Haliotis rubra* share similar food resources in that they both feed on algae; however, these 2 herbivores have very different impacts on this resource. Increases in the density of *C. rodgersii* resulted in declines in the cover and dry weight of total algae, as well as brown and red algae considered separately. In contrast, the presence of *H. rubra* resulted in a slight but not significant decline in the cover and standing biomass of red algae relative to the effect of *C. rodgersii.* This differential reflects differences in their feeding habits and morphology.

Centrostephanus rodgersii is a generalist herbivore that grazes intensively on a range of algae and sessile invertebrates (Andrew et al. 1998). In contrast, *Haliotis rubra* is a specialist herbivore that preferentially traps and/or grazes on red algae with low intensity (Shepherd 1973). Our results demonstrated that *C. rodgersii* has a broader range of dietary preferences and a higher feeding rate than *H. rubra.*

In the enclosures, *Centrostephanus rodgersii* monopolized the algae resources to a greater extent than *Haliotis rubra*, and the impacts of the

urchins on the abalone could have been linked to food shortages. *C. rodgersii* were less affected by such food shortage, because urchins are more efficient at converting low, medium and high densities of algal resources to body weight and are better adapted to survive low abundances of food than abalone (Tegner & Levin 1982, Andrew 1989). These results suggest that the impacts of *C. rodgersii* on *H. rubra* could be linked to exploitative competition for food.

Impacts of *Centrostephanus rodgersii* on *Haliotis rubra*

The incursion of *C. rodgersii* has a negative impact on the abundance, distribution and condition of individual *H. rubra* on the east coast of Tasmania. In previous research, we demonstrated that introducing *C. rodgersii* to intact algal beds causes abalone to emigrate from open plots and to seek shelter in cryptic microhabitats (Chapter 2). The present results suggest that, as *C. rodgersii* establishes at a site, the body condition and survival of *H. rubra* will decline. Clearly then, the establishment of *C. rodgersii* in intact algal beds has important and negative consequences for the abalone fishery prior to any onset of destructive grazing.

A crucial issue in competitive interactions between invasive and native herbivores is whether one species will be excluded. Our results demonstrate an asymmetrical interaction in which *Centrostephanus rodgersii* has a clear impact on *Haliotis rubra*, but the abalone has no detectable effect on the urchin. Nevertheless, it would appear that *C. rodgersii* and *H. rubra* can co-exist in intact algal beds (Andrew & Underwood 1992). It is possible that *C. rodgersii* exclusion of *H. rubra* takes a long time, or that co-existence of *C. rodgersii* and *H. rubra* is linked to an inability of the urchin to inhabit shallow waters (approximately <5 m) at high population densities, where abalone occur in considerable abundance (Johnson et al. 2005), or to an incomplete overlap in food resource utilisation.

Conclusions

Overall, the invader (*Centrostephanus rodgersii*) is the superior competitor in interactions with the native herbivore *Haliotis rubra.* There was no evidence to suggest that *H. rubra* had a similar negative effect on *C. rodgersii.* These results are consistent with other studies on the effects of interspecific competition between native and invasive herbivores, in which the great majority show that the invasive species is the superior competitor in interactions with native herbivores (Berman & Carlton 1991, Carlton 1992,

Byers 2000, Bohn & Amundsen 2001, Bachelet et al. 2004, Steffani & Branch 2005). Our results strongly suggest that superior competitive ability, which is most often likely in a generalist consumer, is an important factor in predicting the impact of invasive herbivores on marine ecosystems (Carlton 1992, Byers 2000).

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CHAPTER 4: DIRECT AND INDIRECT EFFECTS OF RANGE EXPANDING GENERALIST GRAZER ON COMMERCIALLY FISHED ABALONE AND URCHINS

ABSTRACT

The climate change induced range expansion of non-indigenous species can have major impacts on native biota. We used a removal experiment to test the direct and indirect impacts of the range expanding urchin (*Centrostephanus rodgersii*) on populations of 2 commercially fished native species blacklip abalone (*Haliotis rubra*) and the urchin (*Heliocidaris erythrogramma*) in eastern Tasmania, Australia. After 13 months of maintaining the experimental manipulations, densities of juvenile and adult *H. rubra* only increased in the treatments, where *C. rodgersii* were removed and regrowth allowed relative to unmanipulated barrens. In contrast, densities of adult *H. erythrogramma* increased in all treatments where *C. rodgersii* was removed. These results suggest that *C. rodgersii* has a direct negative impact on the densities of juvenile and adult *H. rubra* through competition for food, and on the densities of adult *H. erythrogramma* through competition for shelter. Other indirect impacts were also evident. Densities of adult and juvenile *H. rubra* and adult *H. erythrogramma* were lower in the treatment from which *C. rodgersii* and regrown canopy algae were removed relative to patches from which only *C. rodgersii* was removed. This suggests *C. rodgersii* grazing has an indirect negative effect on the densities of adult and juvenile *H. rubra* and adult *H. erythrogramma* through loss of biogenic habitat. Densities of juvenile *H. erythrogramma* were higher in treatment from which *C. rodgersii* and algal regrowth were removed relative to unmanipulated barrens and patches from which only *C. rodgersii* was removed. These results suggest juvenile *H. erythrogramma* prefer barrens habitat, however *C. rodgersii* has a direct negative impact on the densities of juvenile *H. erythrogramma* through either competition or predation. Our results suggest that *C. rodgersii* will have a direct negative impact on commercial *H. rubra* and *H. erythrogramma* fisheries. The climate induced range expansion of generalist grazers can have disproportionately large impacts on ecosystems structure and function.

Key words: climate change, direct and indirect impacts, *Centrostephanus rodgersii, Haliotis rubra, Heliocidaris erythrogramma,* urchin barrens

INTRODUCTION

Global climate change is leading the poleward range expansion of many non-indigenous marine species (Parmensan 1996, Hickling et al. 2006). Non-indigenous species can alter ecosystems structure and function (e.g. Parmesan & Yorke 2003, Harley et al. 2006) through direct and indirect impacts on native biota (Smith 2005), biogenic habitats (Ling 2008, Firth et al. 2009), biogeochemical cycles, and food webs dynamics (Parmesan & Yorke 2003, Harley et al. 2006). However, the direct and indirect effects of many non-indigenous species are not well understood (Carlton 1992, Carlton & Geller 1993, Ruiz et al. 1999).

Driven by increased poleward penetration of the East Australian Current (Ridgway 2007) the long spined urchin *Centrostephanus rodgersii* has undergone a southerly range expansion from New South Wales and was first recorded in mainland Tasmanian waters in 1978 (Edgar 1997, Johnson et al. 2005, Ling & Johnson 2009). This urchin is well known for its ability to overgraze algal beds, affecting a catastrophic shift to barrens habitat dominated by the urchin and characterised by bare rock (Johnson et al. 2005, Ling 2008) or, in its endemic range encrusting red algae (ERA) (Fletcher 1987). *C. rodgersii* barrens are becoming more widespread along the south east coast of Australia, and do not support viable commercial fisheries of blacklip abalone *Haliotis rubra* and the urchin *Heliocidaris erythrogramma* (Andrew & Underwood 1992, Andrew et al. 1998, Johnson et al. 2005). These results suggest *C. rodgersii* has a negative impact on populations of *H. rubra* and *H. erythrogramma,* although the mechanisms remain unclear (Andrew & Underwood 1992, Andrew et al. 1998, Johnson et al. 2005).

The direct and indirect impacts of *C. rodgersii* on *H. rubra* and *H. erythrogramma* may vary between their life stages. The direct impacts of *C. rodgersii* could include competition with adult and/or juvenile *H. rubra* and *H. erythrogramma* for food (Shepherd 1973a, Tegner & Levin 1982) or shelter (Andrew et al. 1998), and direct consumption of juvenile *H. rubra* and *H. erythrogramma* (McShane 1991). The potential indirect impacts of *C. rodgersii* on *H. rubra* and *H. erythrogramma* are more complex and difficult to predict. *C. rodgersii* grazing has a major influence on the structure of algal beds. Loss of structural complexity may result in increased predation pressure (Edgar et al. 2004, Andrew & Byrne 2005). Alternatively, since grazing by *C. rodgersii* in some areas can be important in maintaining ERA

which provide an important settlement cue for urchin and abalone larvae, and the benthic microflora and diatoms that grown on ERA are also part of the early diet of juvenile *H. erythrogramma* and *H. rubra* (Shepherd 1973b, Morse & Morse 1984, Shepherd & Turner 1985, Daume et al. 1999), it is possible that *C. rodgersii* grazing may act to promote densities of juvenile *H. rubra* and *H. erythrogramma* at local scales (Andrew & Underwood 1992). We used a removal experiment to test the direct and indirect impacts of *C. rodgersii* on reef habitat structure and on the abundances of commercially fished native species *H. rubra* and *H. erythrogramma,* in eastern Tasmania, Australia.

MATERIALS AND METHODS

Study site characteristics

The experiment was undertaken at the Lanterns on the east coast of Tasmania, Australia, between August 2005 and September 2006 (Figure 1). Two sites, approximately 0.5 km apart, were selected randomly from several possible sites in the area. Reefs at the sites support incipient urchin barrens (i.e. dense algal beds with scattered patches of barrens habitat caused and maintained by *Centrostephanus rodgersii* grazing). Both sites have steeply sloping rocky substratum to a depth of >30 m and, based on the classification scheme proposed by Edgar (1984), are moderately exposed.

Experimental design

At each site, 12 *C. rodgersii* barrens patches at 12-19 m depth were selected randomly. Patch length and width were measured and the outer perimeter marked with yellow flagging tape (length mean=5.02 m, +/-SE=0.12 m and width mean=5.14 m, +/-SE=0.1 m). Each barrens patch was then assigned randomly to the following treatments: T1=unmanipulated *C. rodgersii* barrens; T2=removal of *C. rodgersii* and all regrowth; T3=removal of *C. rodgersii* and canopy algae regrowth; and T4=removal of only *C. rodgersii.* Control treatment, in intact algal beds unaffected by *C. rodgersii* grazing, were also selected randomly and delineated with flagging tape to be of similar size to barren patches (T5). There were 3 replicate plots of each of the 5 treatments at each site.

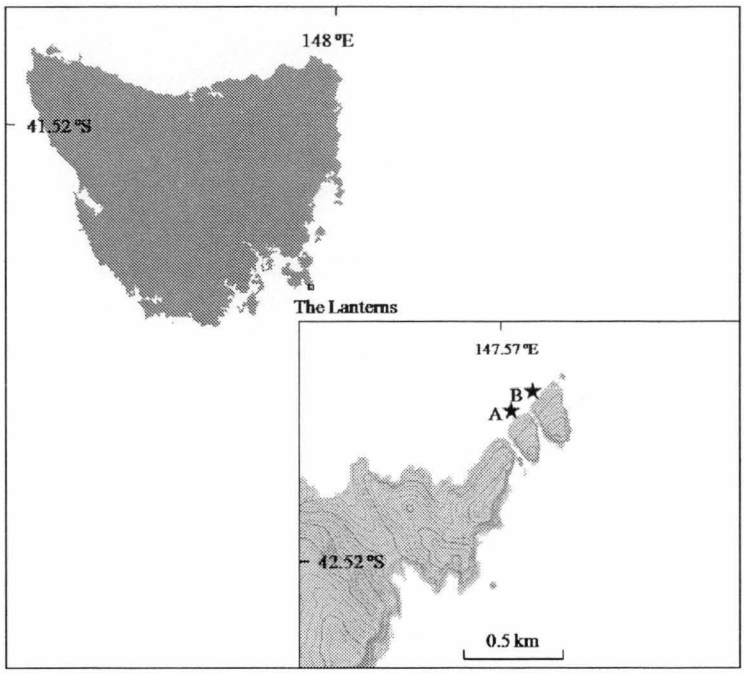

Figure 1. Map of the east coast of Tasmania, Australia, showing the 2 study sites at the Lanterns.

At the beginning of the experiment all *C. rodgersii* were removed from relevant treatments patches by divers, and experimental conditions were maintained thereafter by monthly visits. For the treatment where *C. rodgersii* and all regrowth were removed, filamentous and turfing algae and sessile invertebrates were removed from patches using a copper wire bush, while canopy algae (≥300 mm), including their holdfasts were removed by hand. To avoid edge effects, response variables were not monitored within 1 m of the edge of the patch.

Densities of *C. rodgersii*, *Heliocidaris erythrogramma* and *Haliotis rubra*

At both sites, the densities (per m^2) of urchins (*C. rodgersii* and *H. erythrogramma*) and abalone (*H. rubra*) in each patch was assessed immediately prior to experimental manipulations, 1 month after establishing the treatments, and then at two monthly intervals over thirteen months. Patch area was calculated using the formula for an ellipsoid (Pix(LxW)). On each sampling occasion, *H. erythrogramma* test width and *H. rubra* shell length

were measured *in situ* using vernier calipers. Densities were determined as total densities for *C. rodgersii,* while densities of juveniles and adults were estimated separately for *H. erythrogramma* (juveniles <60 mm and adult ≥60 mm test width diameter) and *H. rubra* (juveniles <60 mm and adult ≥60 mm shell length).

Sampling

The percentage cover and density of overstorey algae, and percentage cover of bare rock, understorey algae and sessile invertebrates, were assessed immediately prior to experimental manipulations and then at regular intervals throughout the experiment. Due to time constraints, the sampling interval differed between the two sites. At the first site, the community was first assessed immediately prior to experimental manipulations, one month latter and then at two monthly intervals for a further twelve months. At the second site, the community was assessed immediately prior to experimental manipulations and then at seven and thirteen months after the initial experimental manipulations. At both sites, the assessment took place in a two-stage process, using a modification of the methods of Valentine and Johnson (2003).

Overstorey algae were assessed in terms of both stipe counts (density) and the percentage cover of each species. Stipe counts involved recording all adult plants (≥300 mm in height) inside the buffer area of each patch. The percentage cover of overstorey algae was then estimated by eye in four randomly positioned 0.5x0.5 m quadrats. The fronds of these plants were then moved aside to allow assessment of the percentage cover of understorey algae, sessile invertebrates and bare rock by photography. The cover of understorey species was estimated from digitised photos using a point intercept method, in which a grid of 100 equidistant points was overlain on each photo and the identify of organisms at each point determined. All photographic quadrat analyses were undertaken using Microsoft Photoshop Software. Note that given multiple layers in the structure of the seaweed community (e.g. canopy and sub canopy algae overlay understorey species), total algal cover of individual patches can exceed 100%. Canopy-forming algae were identified to species while understorey algae were identified to divisions (e.g. brown or red algae).

Analysis

The effect of the different treatments on the total densities of *C. rodgersii* and the densities of adult and juvenile *H. erythrogramma* and *H. rubra* were analysed 13 months after experimental manipulations (September 2006) using 2-way ANOVAs. The model included the main effects of treatment (fixed, 5 levels=T1-T5) and sites (random, 2 levels=Site 1 and 2) and their interaction.

The effect of the different treatments on the density of stipes of total overstorey algae and the individual canopy-forming species were analysed 13 months after the initial experimental manipulations using 2-way ANOVAs (see above details).

The effects of the treatments on the percentage cover of overstorey and understorey algae, bare rock and sessile invertebrates (13 months after initial manipulations) were analysed with 3-way nested ANOVAs. The models included the main effects of treatment (fixed, 5 levels=T1-T5) and sites (random, 2 levels), their interaction and patch (random, 3 levels=3 patches) nested within treatment x site.

The effect of the treatments on patches community structure was analysed immediate prior and thirteen months after initial manipulations, using 2-way PERMANOVAs (see above model). To depict the community structure, we used non-metric multi-dimensional scaling (nMDS) plots. These analyses were based on Bray-Curtis similarity matrices derived from percentage cover data after a 4^{th} root transformation to reduce the influence of dominant species, using the Primer 6.0 Software.

Prior to all univariate tests, transformations to stabilize variances were determined from the relationship between group standard deviations and means. Variables that were transformed are expressed in terms of the untransformed variable *Y*. Where significant differences were found in the overall tests, planned comparisons between treatments were made (Table 1). For all a priori comparisons we adjusted α using the procedure suggested by Todd and Keough (1994). All univariate tests and graphical representations were undertaken using the statistical software R.

Table 1. Details of planned comparisons to test the effect the experimental manipulations on the benthic habitat and densities of *C. rodgersii H. rubra* and *H. erythrogramma* in treatment patches (mean 30.654 m^2, +/- SE 0.63 m^2) after 13 months of experimental manipulations. Treatments are, T1=unmanipulated *C. rodgersii* barrens, T2=removals of *C. rodgersii* and all regrowth from patches, T3=removals of *C. rodgersii* and canopy algae regrowth from patches, T4=removals of only *C. rodgersii* from patches, T5=no *C. rodgersii* in intact algal patches.

Comparisons	Rationale
Benthic structure	
T2=T1	Simulated barrens are similar to unmanipulated barrens
T2≠T5	Simulated barrens are significantly different to intact algal patches
T3≠T1	Canopy removal patches are significantly different to unmanipulated barrens
T3≠T5	Canopy removal patches are significantly different to intact algal patches
T4≠T1	Regrown barrens are significantly different to unmanipulated barrens
T4=T5	Regrown barrens are similar to intact algal patches
Overstorey algae	
T2=T1	Simulated barrens are similar to unmanipulated barrens
T2<T5	Simulated barrens have less cover than intact algal patches
T3=T1	Canopy removal patches are similar cover to unmanipulated barrens
T3<T5	Canopy removal patches have less cover than intact algal patches
T4>T1	Regrown barrens have more compared to unmanipulated barrens
T4=T5	Regrown barrens are similar to intact algal patches
Bare rock and ERA	
T2=T1	Simulated barrens are similar to unmanipulated barrens
T2>T5	Simulated barrens have high cover than intact algal patches
T3<T1	Canopy removal patches have less cover than unmanipulated barrens
T3=T5	Canopy removal patches are similar to intact algal patches
T4<T1	Regrown barrens have less cover than unmanipulated barrens
T4=T5	Regrown barrens are similar to intact algal patches
Juvenile overstorey and understorey algae and sessile invertebrates	
T2=T1	Simulated barrens are similar to unmanipulated barrens
T2<T5	Simulated barrens have less cover than intact algal patches

T3>T1	Canopy removal patches have higher cover than unmanipulated barrens
T3=T5	Canopy removal patches are similar to intact algal patches
T4>T1	Regrown barrens have high cover than unmnaipulated barrens
T4=T5	Regrown barrens are similar to intact algal patches
C.rodgersii	
T2,T3,T4<T1	Lower density in treatment patches than in unmanipulated barrens
T5<T1	Higher density in unmanipulated barrens than in intact algal patches
T2,T3,T4=T5	Similar density in treatment patches to that in intact algal patches
Adult *H. erythrogramma* and *H. rubra*	
T3,T4>T1	Higher density in canopy barrens and regrown barrens, than in unmanipulated barrens, because these species compete for food
T3,T4=T5	No detectable differences between canopy barrens and regrown barrens and intact algal patches, because these species compete for food
T2>T1	Higher density in simulated barrens than unmanipulated barrens, because these species compete for shelter
T2=T5	No detectable differences between simulated barrens and intact algal patches, because these species compete for shelter
T3<T4	Higher density in regrown barrens than canopy barrens because these species depend on canopy algae for protection from predators
Juvenile *H. erythrogramma* and *H. rubra*	
T2,T3,T4>T1	Higher density in treatment patches than unmanipulated barrens because adult *C. rodgersii* preys on juvenile *H. erythrogramma* and *H. rubra*
T4<T2	Lower density in regrown barrens than simulated barrens because juvenile *H. erythrogramma* and *H. rubra* depend on ERA for settlement cues, food and protection and/or avoid sediment, invertebrates and algae

RESULTS

A summary of the results is given in Table 2. Detailed results are outlined below.

Table 2. Relative amount and cover of benthic habitat and densities of *Centrostephanus rodgersii, Haliotis rubra* and *Heliocidaris erythrogramma* in treatment patches prior to experimental manipulations (August 2005) and 13 months after (September 2006).

Response Variable	**Treatments**				
	T1	T2	T3	T4	T5
Overstorey algae					
Aug05	L	L	L	L	H
Sep 06	L	L	L	**H**	H
Bare rock					
Aug05	H	H	H	H	L
Sep 06	H	H	**M**	**L**	L
ERA					
Aug05	L	L	L	L	H
Sep 06	L	L	L	L	H
Filamentous algae					
Aug05	L	L	L	L	H
Sep 06	L	**M**	**M**	**M**	H
Understorey foliose algae					
Aug05	L	L	L	L	H
Sep 06	L	L	**H**	**H**	H
Sessile invertebrates					
Aug05	L	L	L	L	M
Sep 06	L	**M**	**M**	**M**	M
C. rodgersii					
Aug05	H	H	H	H	L
Sep 06	H	**L**	**L**	**L**	L
Adult *H. rubra*					
Aug05	L	L	L	L	H
Sep 06	L	L	**M**	**H**	H
Juvenile *H. rubra*					
Aug05	L	L	L	L	H
Sep 06	L	L	**M**	**H**	H
Adult *H. erythrogramma*					
Aug05	L	L	L	L	L
Sep 06	L	**M**	**M**	**H**	L
Juvenile *H. erythrogramma*					
Aug05	L	L	L	L	L
Sep 06	L	**H**	L	L	L

Density of *Centrostephanus rodgersii*

At the beginning of the experiment, the density of *C. rodgersii* in all barrens patches was similar, and much higher than the patches in intact algal beds (Figure 2). After 13 months of removing *C. rodgersii*, the density of *C. rodgersii* was significantly higher in the unmanipulated barrens patches than in the patches from which the urchins were removed (Figure 2, Table 3). There were no detectable differences in the density of *C. rodgersii* between the treatment patches where the urchin was removed and the patches in intact algal beds (Figure 2, Table 3).

Table 3. *Centrostephanus rodgersii*. Results are the overall 2-way ANOVAs and planned comparisons testing the effect the treatments on the densities of *C. rodgersii* in treatment patches (mean 30.654 m^2, +/- SE 0.63), 13 months after experimental manipulations (September 2006). Significant p-values are shown in bold print: $p<0.05$ are significant for the main analysis and $p<0.007$ are significant for planned comparisons.

Factors	**df**	**MS**	***F***	**p**	**Comparisons**	***T***	**p**
Treatment	4	1.125	926.179	**$3e^{-6}$**	T2,T3,T4<T1	-58.52	**$<2e^{-16}$**
Site	1	0.003	2.593	0.189	T5<T1	-36.6	**$2e^{-12}$**
Treatment x Site	4	0.001	1.429	0.261	T2,T3,T4<T5	-0.973	0.341
Error	20	0.001					

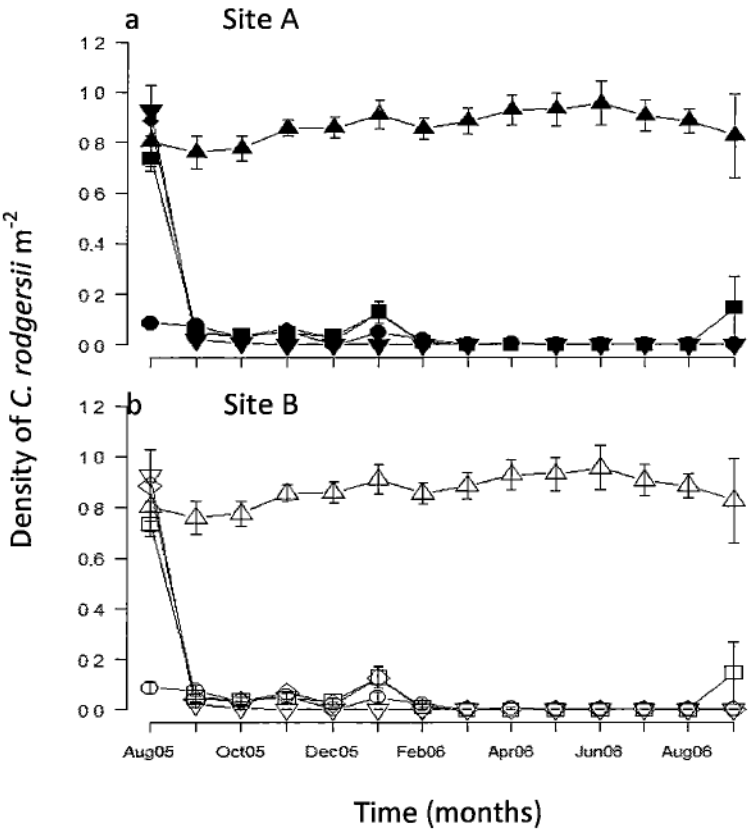

Figure 2. *Centrostephanus rodgersii.* Mean density (+/- SE) of *C. rodgersii* (m^2) through time (months), at both sites at the Lanterns. Treatments are, upright triangles=unmanipulated *C. rodgersii* barrens patches, diamonds=removals of *C. rodgersii* and all regrowth from patches, downward triangles=removals of both *C. rodgersii* and canopy algae regrowth from patches, squares=removals of only *C. rodgersii* from patches, circles=no *C. rodgersii* in intact algal patches, n=3 replicates for each (see Table 3 for ANOVA results).

Density of adult and juvenile *H. rubra*

Prior to the experimental manipulations, the density of adult and juvenile *H. rubra* in the *C. rodgersii* barrens patches was similar, and much lower than in the patches in intact algal beds (Figures 3, 4).

After 13 months, there were notable differences in the densities of adult and juvenile *H. rubra* between treatments (Figures 3, 4, Table 4). There was a significantly higher density of adult and juvenile *H. rubra* in the treatments patches from which only *C. rodgersii* was removed, and from which *C. rodgersii* and canopy algae regrowth were removed, than in the unmanipulated *C. rodgersii* barrens patches (Figure 3, 4, Table 4).

There was also a significantly lower density of both adult and juvenile *H. rubra* in the treatment patches where both *C. rodgersii* and canopy algae regrowth were removed relative to the patches where only *C. rodgersii* was removed (Figures 3, 4, Table 4). The density of adult and juvenile *H. rubra* in patches where only *C. rodgersii* was removed and the in intact algal beds were similar (Figures 3, 4, Table 4). In contrast there was a significantly lower density of adult and juvenile *H. rubra* in the treatment from which *C. rodgersii* and all regrowth were removed than in the intact algal patches (Figures 3, 4, Table 4). There were no detectable differences in the density of adult and juvenile *H. rubra* between the treatment patches from which *C. rodgersii* and all regrowth were removed and the unmanipulated *C. rodgersii* barrens patches (Figures 3, 4, Table 4). The density of juvenile *H. rubra* was lower in the treatment patches where *C. rodgersii* and all regrowth were removed than in the patches where only *C. rodgersii* was removed (Figures 3, 4, Table 4). There were no discernable differences in the density of juvenile *H. rubra* between all the combined treatments in which *C. rodgersii* was removed and the unmanipulated *C. rodgersii* barrens patches (Figures 3, 4, Table 4).

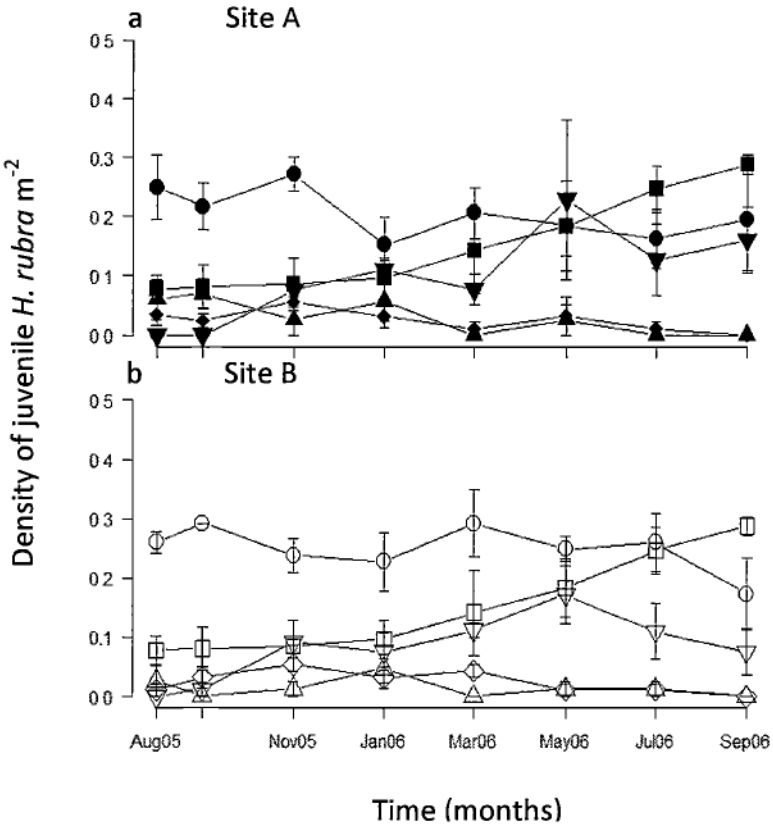

Figure 3. *Haliotis rubra.* Mean densities (+/-SE) of juvenile *H. rubra* (m^2) in through time (months), at the Lanterns. Treatments are, upright triangles=unmanipulated *C. rodgersii* barrens patches, diamonds=removals of *C. rodgersii* and all regrowth from patches, downward triangles=removals of both *C. rodgersii* and canopy algae regrowth from patches, squares=removals of only *C. rodgersii* from patches, circles=no *C. rodgersii* in intact algal patches, *n*=3 replicates for each (see Table 4 for ANOVA results).

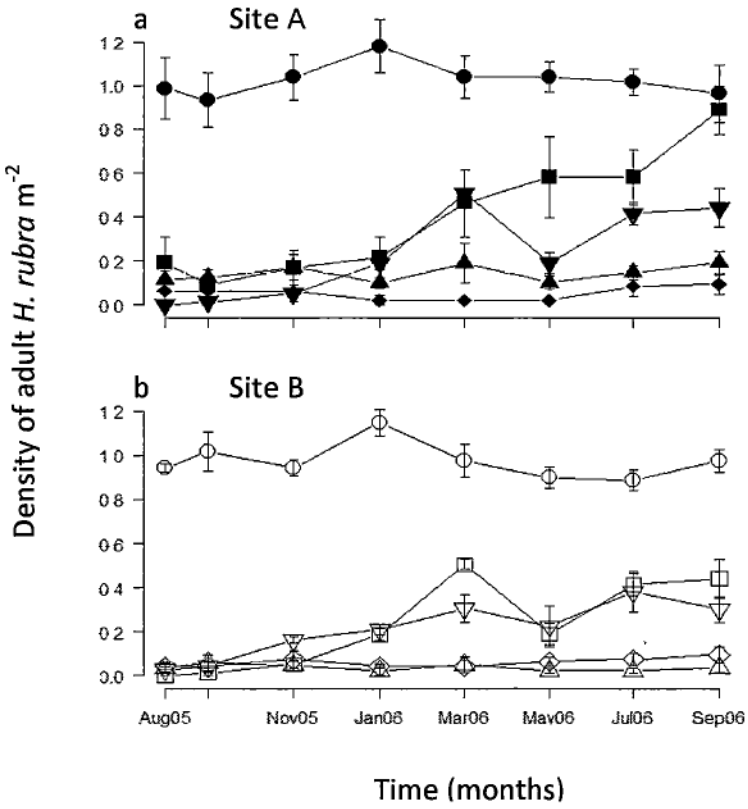

Figure 3. *Haliotis rubra.* Mean densities (+/-SE) of adult *H. rubra* (m^2) through time (months), at the Lanterns. Treatments are, upright triangles=unmanipulated *C. rodgersii* barrens patches, diamonds=removals of *C. rodgersii* and all regrowth from patches, downward triangles=removals of both *C. rodgersii* and canopy algae regrowth from patches, squares=removals of only *C. rodgersii* from patches, circles=no *C. rodgersii* in intact algal patches, n=3 replicates for each (see Table 4 for ANOVA results).

Table 4. *Haliotis rubra*. Results are the overall 2-way ANOVAs and planned comparisons testing the effect of treatments on the densities of juvenile and adult *H. rubra* in treatment patches (mean 30.654 m^2, +/- SE 0.63), 13 months after experimental manipulations (September 2006). Significant p-values are shown in bold print: $p<0.05$ are significant for the main analysis and $p<0.015$ are significant for testing the effect of treatments on juveniles and $p<0.025$ are significant for testing the effect of treatments on adults (α adjusted using Todd and Keough (1994)).

Factors	**df**	**MS**	***F***	**p**	**Comparisons**	***T***	**p**
Juvenile [log(y+0.001)]							
Treatment	4	45.959	45.133	**0.001**	T2>T1	0.231	0.49
Site	1	0.909	0.893	0.458	T2=T5	-9e-15	**<2-e^{16}**
Treatment x Site	4	1.018	1.106	0.381	T3<T4	-2.018	**0.004**
Error	20	0.921			T2,T3,T4>T1	2.219	0.019
					T4<T2	-10.97	0.457
Adult					T3,T4>T1	12.46	**0.001**
Treatment	4	0.898	36.43	**0.002**	T3,T4=T5	3.554	**0.003**
Site	1	0.102	4.126	0.1	T2>T1	-0.347	0.436
Treatment x Site	4	0.025	1.439	0.258	T2=T5	12.725	**1e^{-7}**
Error	20	0.017			T3<T4	-3.434	**0.003**

Density of juvenile and adult *H. erythrogramma*

At the beginning of the study, the density of juvenile and adult *H. erythrogramma* in all patches was similar (Figure 5, 6, Table 5). After 13 months, there was clear evidence of adult and juvenile *H. erythrogramma* responding to the treatments (Figures 5, 6, Table 5). Densities of both juvenile and adult *H. erythrogramma* were greater in the treatment patches where only *C. rodgersii* was removed, and where *C. rodgersii* and canopy algae regrowth were removed, than in the unmanipulated *C. rodgersii* barrens patches and intact algal patches (Figures 5, 6, Table 5). There was also a higher density of adult and juvenile *H. erythrogramma* in the treatment patches in which *C. rodgersii* and all regrowth were removed relative to the unmanipulated *C. rodgersii* barrens patches and the patches in intact algal beds (Figures 5, 6, Table 5). In contrast, there was a slight but not significantly higher density of juvenile *H. erythrogramma* in the combined treatment patches where *C. rodgersii* was removed than in the unmanipulated *C. rodgersii* barrens patches (Figures 5, 6, Table 5). In the treatment patches where both *C. rodgersii* and canopy algae regrowth were removed, densities of adult *H. erythrogramma* were lower than in the patches where only *C. rodgersii* was removed (Figures 5, 6, Table 5). In contrast, there were no detectable differences in the density of juvenile *H. erythrogramma* between these treatment patches (Figures 5, 6, Table 5). There was a higher density of juvenile *H. erythrogramma* in treatment patches from which *C. rodgersii* and all regrowth was removed than in the patches where only *C. rodgersii* was removed (Figures 5, 6, Table 5).

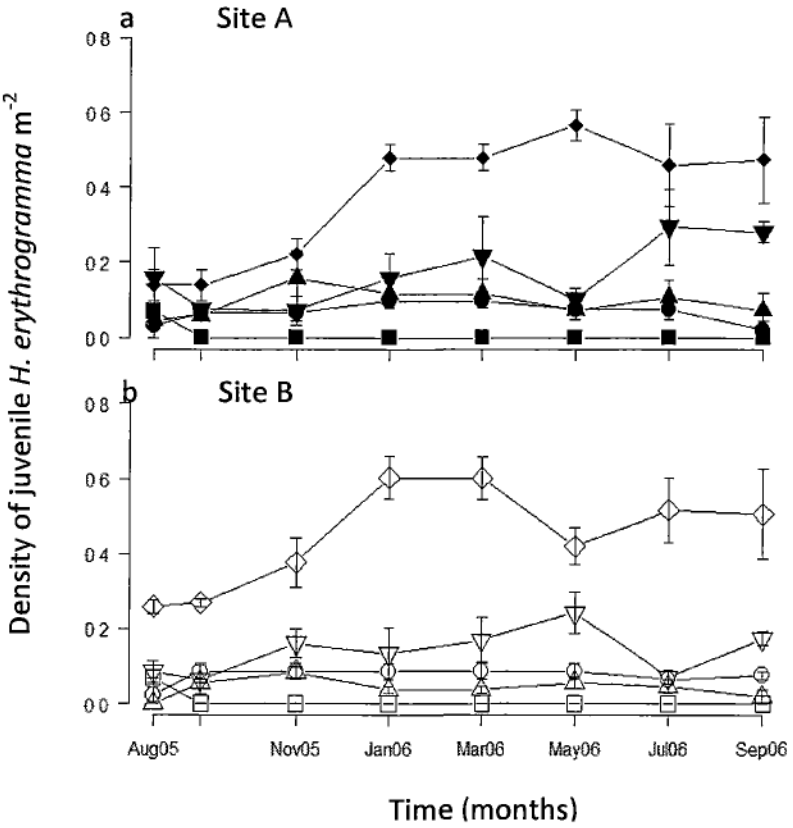

Figure 5. *Heliocidaris erythrogramma.* Mean densities (+/-SE) of juvenile *H. erythrogramma* (m^2) through time (months), at the Lanterns. Treatments are, upright triangles=unmanipulated *C. rodgersii* barrens patches, diamonds=removals of *C. rodgersii* and all regrowth from patches, downward triangles=removals of both *C. rodgersii* and canopy algae regrowth from patches, squares=removals of only *C. rodgersii* from patches, circles=no *C. rodgersii* in intact algal patches, n=3 replicates for each (see Table 5 for ANOVA results).

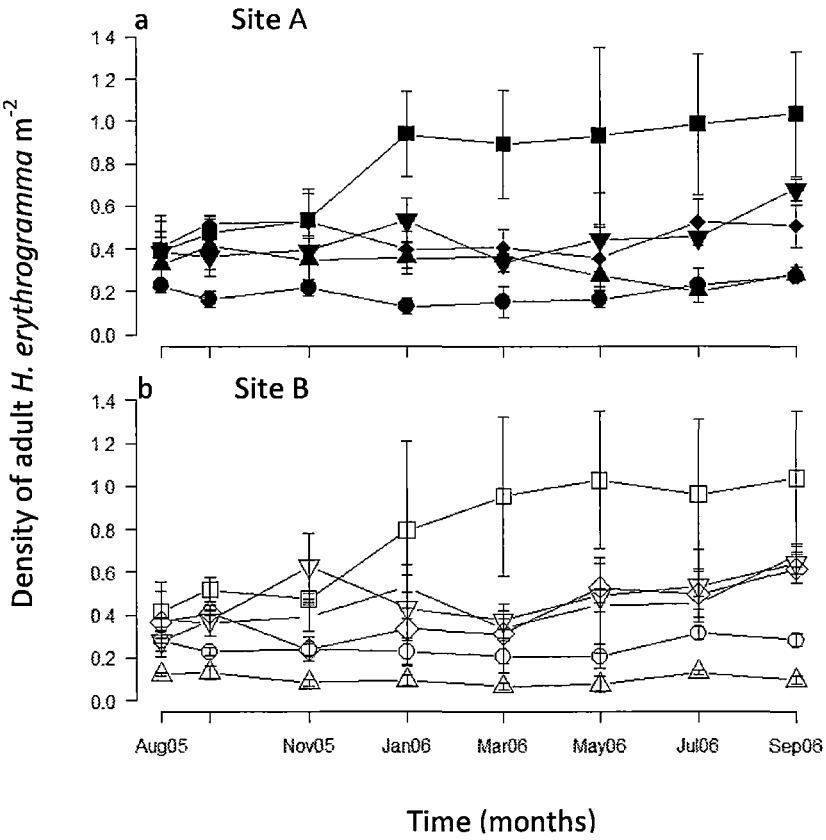

Figure 6. *Heliocidaris erythrogramma.* Mean densities (+/-SE) of adult *H. erythrogramma* (m^2) through time (months), at the Lanterns. Treatments are, upright triangles=unmanipulated C. rodgersii barrens patches, diamonds=removals of *C. rodgersii* and all regrowth from patches, downward triangles=removals of both C. *rodgersii* and canopy algae regrowth from patches, squares=removals of only *C. rodgersii* from patches, circles=no *C. rodgersii* in intact algal patches, n=3 replicates for each (see Table 5 for ANOVA results).

Table 5. *Heliocidaris erythrogramma*. Results are the overall 2-way ANOVAs and planned comparisons testing the effect of treatments on the densities of juvenile and adult *H. erythrogramma* in treatment patches (mean 30.654 m^2, +/- SE 0.63), 13 months after experimental manipulations (September 2006). Significant p-values are shown in bold print: $p<0.05$ are significant for the main analysis and $p<0.015$ are significant for testing the effect of treatments on juveniles and $p<0.025$ are significant for testing the effect of treatments on adults (α adjusted using Todd and Keough (1994)).

Factors	**df**	**MS**	***F***	**p**	**Comparisons**	***T***	**p**
Juvenile					T3,T4>T1	-4.485	**0.001**
Treatment	4	0.199	27.532	0.003	T3,T4=T5	-4.825	**0.001**
Site	1	0.001	0.042	0.005	T2>T1	5.631	**0.001**
Treatment x Site	4	0.007	0.725	0.415	T2=T5	-5.777	**0.001**
Error	20	0.01			T3<T4	2.019	**0.465**
					T2,T3,T4>T1	-3.184	**0.04**
					T4<T2	4.296	**$5e^{-4}$**
Adult [log(y+0.001)]					T3,T4>T1	-2.843	**0.001**
Treatment	4	3.218	8.3	0.032	T3,T4=T5	-9.79	**$1e^{-6}$**
Site	1	0.087	0.223	0.088	T2>T1	4.211	**0.002**
Treatment x Site	4	0.388	4.164	0.013	T2=T5	-4.624	**0.001**
Error	20	0.093			T3<T4	-2.16	**0.024**

Benthic community structure

Prior to experimental manipulations in August 2005, the community structure in all *C. rodgersii* barrens patches was similar and distinctly different to that of the unmanipulated control patches in intact algal beds (Figure 7).

After 13 months, there was clear separation in MDS space between the treatment patches (Figure 7, Table 6). Although there was some variability in the response between sites and between individual patches subject to the same treatment within sites, the community structure in patches from which both *C. rodgersii* and canopy algae regrowth were removed and from which only *C. rodgersii* was removed, were consistently different to the unmanipulated *C. rodgersii* barrens (Figure 7, Table 6). The patches from which both *C. rodgersii* and canopy algae regrowth were removed were also distinctly different to the intact algal patches (Figure 7, Table 6). In contrast, there no detectable differences in community structure between the patches where only *C. rodgersii* was removed and where *C. rodgersii* and canopy algae regrowth were removed and the intact algal patches (Figure 7, Table 6). There was also clear separation in MDS space in the community structure between the treatment where *C. rodgersii* and all regrowth was removed and the unmanipulated *C. rodgersii* barrens (Figure 7, Table 6). This reflects an increase in the cover of filamentous algae in this treatment compared with the unmanipulated *C. rodgersii* barrens. There were, however distinct differences in the community structure between the treatment patches and the intact algal patches (Figure 7, Table 6).

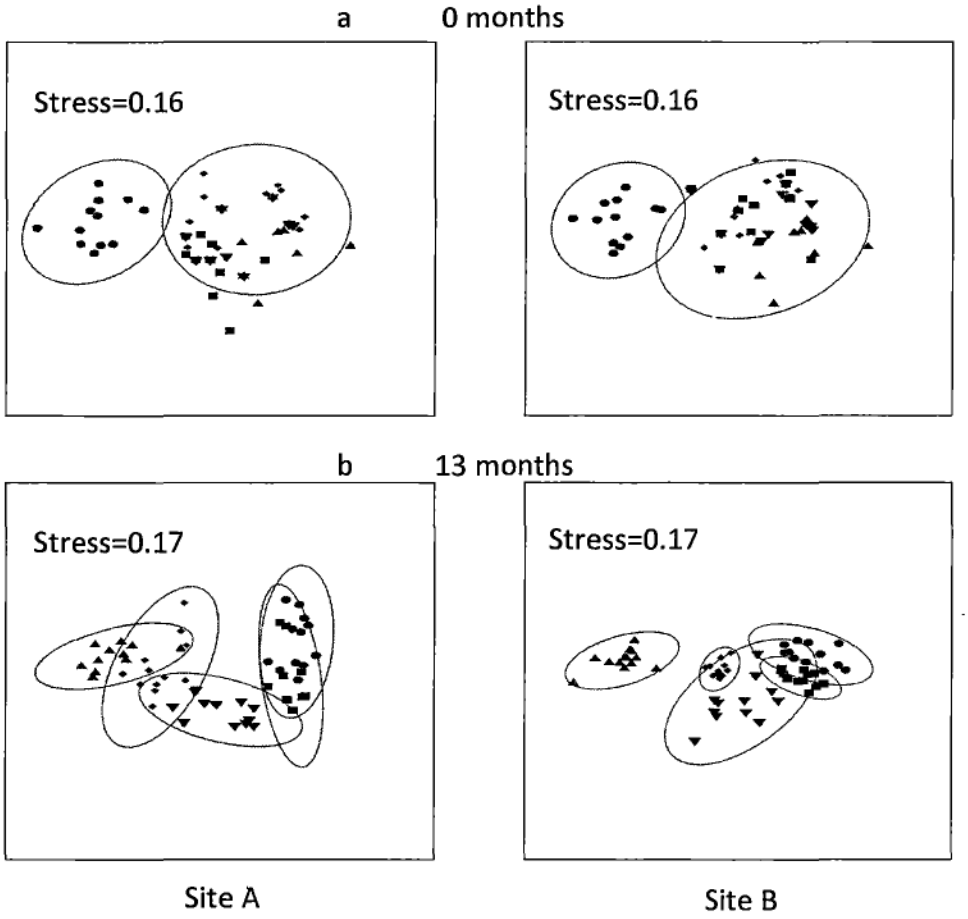

Figure 7. Ordinations (nMDS) of benthic community structure, showing the relationship between experimental treatments (n=3) at (a) 0 months prior to manipulations (August 2005), and (b) 13 months after initial manipulations (September 2006), at site A and site B at the Lanterns. Treatments are, upright triangles=unmanipulated *C. rodgersii* barrens patches, diamonds=removals of *C. rodgersii* and all regrowth from patches, downward triangles=removals of both *C. rodgersii* and canopy algae regrowth from patches, squares=removals of only *C. rodgersii* from patches, circles=control no *C. rodgersii* in intact algal patches. The analysis is based on a Bray-Curtis matrix of 4^{th} transformed percentage cover data. Ellipses (95% Confidence interval) are drawn around barrens and control patches in (i) and around all treatments in (ii) for clarity (see Table 6 for PERMAOVA results).

Table 6. Benthic community. Results of 2-way PERMOVAs and planned comparisons testing the effect of the experimental manipulations on the benthic community structure in treatment patches (mean 30.654 m^2, +/- SE 0.64 m^2) 13 months after experimental manipulations (September 2006). Significant p-values are shown in bold print: $p<0.05$ are significant for the main analysis and $p<0.0125$ are significant for the planned comparisons (α adjusted using Todd & Keough (1994)).

Factors	**df**	**MS**	***F***	**p**	**Comparisons**	***T***	**p**
Treatment	4	20883.59	11.872	**0.001**	T2=T1	3.557	**0.01**
Site	1	1964.748	2.837	0.06	T2≠T5	6.15	**0.008**
Treatment x Site	20	1759.062	2.54	**0.016**	T3≠T1	10.518	**0.006**
Plot (Treatment x Site)	4	692.542	2.04	**0.001**	T3≠T5	3.348	**0.01**
Error	119	339.484			T4≠T1	5.006	**0.01**
					T4=T5	1	0.562

Results are comparisons between treatments for each site based on Bray Curtis matrix fourth root transformed data (9999 permutations used for tests of significance).

Bare rock, encrusting red (ERA), understorey and juvenile canopy-forming algae, and sessile invertebrates

After 13 months of removing only *C. rodgersii* from patches, there were no detectable differences in the amount of bare rock and the cover of foliose red, juvenile canopy algae, understorey foliose brown algae and sessile invertebrates relative to the intact algal patches (Figures 8, 9, Table 7). There was however still a significantly lower cover of ERA and filamentous algae in the treatment patches compared with the intact algal patches (Figures 8, 9, Table 7). Removals of *C. rodgersii* and all regrowth from patches to simulated barrens resulted in a significantly lower cover of bare rock, but more sessile invertebrates compared with unmanipulated *C. rodgersii* barrens patches (Figures 8, 9, Table 7). There were no detectable differences in the cover of ERA, juvenile canopy algae, and understorey foliose brown and red algae between the treatment patches and the unmanipulated *C. rodgersii* barrens patches (Figures 8, 9, Table 7). There was however significantly more bare rock, and a lower cover of ERA, juvenile canopy algae and foliose understorey brown and red algae and sessile invertebrates in the treatment patches when compared to the patches in intact algal beds (Figures 8, 9, Table 7). Removals of *C. rodgersii* and canopy algae from patches resulted in significantly less bare rock but a greater cover of filamentous, juvenile canopy-forming algae and foliose understorey brown and red algae than in the unmanipulated *C. rodgersii* barrens patches. There were no detectable differences in the cover of foliose red algae and sessile invertebrates in the treatment patches when compared with the unmanipulated *C. rodgersii* barrens patches. There was significantly more bare rock and juvenile canopy algae and a lower cover of ERA, filamentous and foliose understorey brown algae in the treatment patches than in the intact algal patches (Figures 8, 9, Table 7).

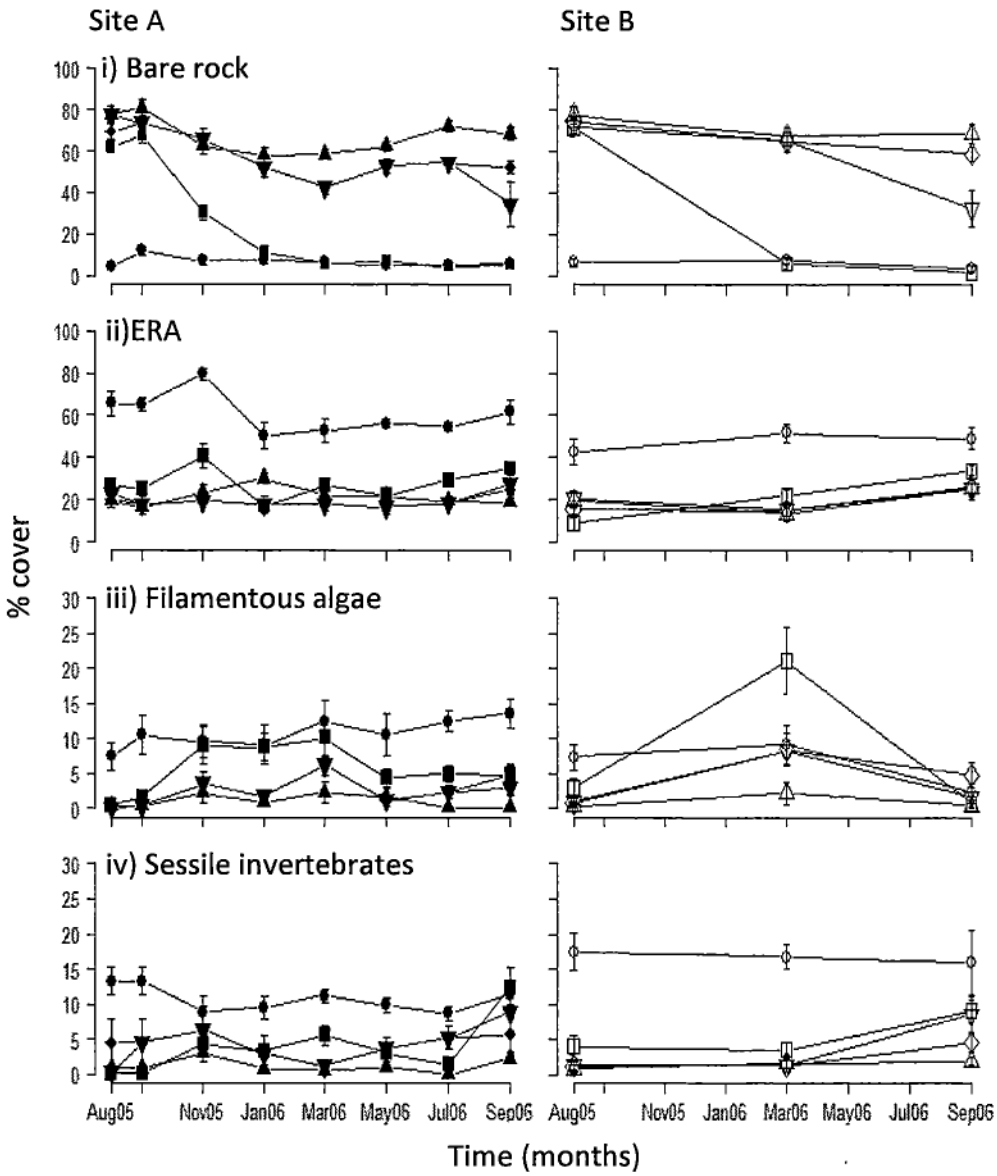

Figure 8. Mean cover (+/-SE) of (i) bare rock, (ii) encrusting red algae (ERA), (iii) filamentous algae and (iv) sessile invertebrates through time (months) through time, at the Lanterns. Treatments are, upright triangles=unmanipulated *C. rodgersii* barrens, diamonds=removals of *C. rodgersii* and all regrowth from patches, downward triangles=removals of both *C. rodgersii* and canopy algae regrowth from patches, squares=removals of only *C. rodgersii* from patches, circles=control no *C. rodgersii* in intact algal patches, n=3 replicates for each (see Table 7 for ANOVA results).

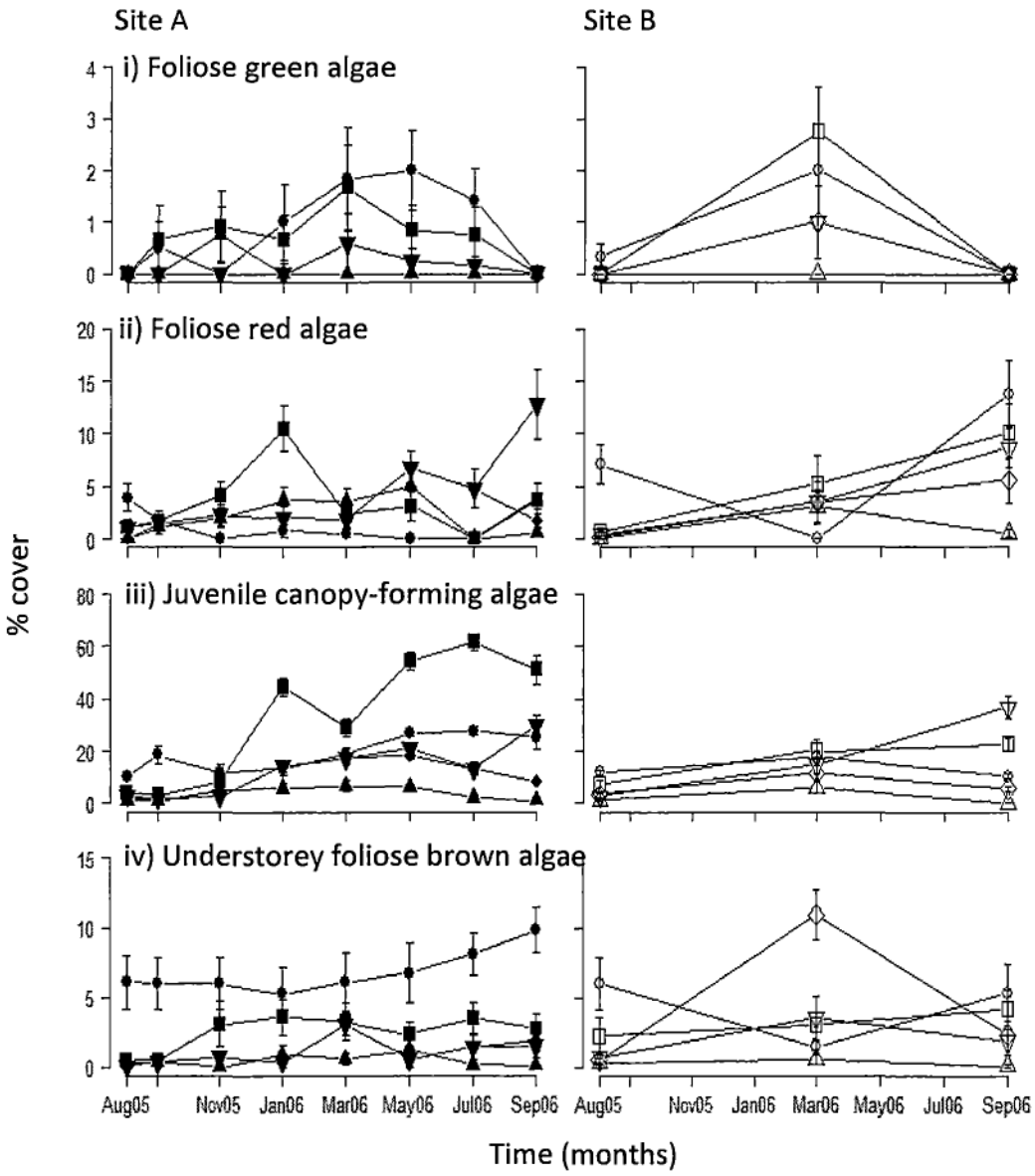

Figure 9. Mean cover (+/-SE) of (i) foliose green algae (ii) foliose red algae, (iii) juvenile canopy forming algae and (iv) understorey foliose brown algae through time (months), at the Lanterns. Treatments are, upright triangles=unmanipulated *C. rodgersii* barrens patches, diamonds=removals of *C. rodgersii* and all regrowth from patches, downward triangles=removals of both *C. rodgersii* and canopy algae regrowth from patches, squares=removals of only *C. rodgersii* from patches, circles=control no *C. rodgersii* in intact algal patches, n=3 replicates for each (see Table 7 for ANOVA results).

Table 7: Understorey community. Results of 2-way ANOVAs and planned comparisons testing the effect of experimental manipulations on the cover of bare rock and encrusting red algae (ERA), filamentous algae and sessile invertebrates in treatment patches. Significant p-values are shown in bold print: $p<0.05$ are significant for the main analysis and $p<0.0125$, are significant for the planned comparisons (α adjusted using Todd and Keough (1994)).

Factors	**df**	**MS**	***F***	**p**	**Comparisons**	***T***	**p**
Bare rock					T2=T1	-3.606	**0.001**
Treatment	4	20762	218.674	**$7e^{-5}$**	T2>T5	-20.99	**$<2e^{-16}$**
Site	1	2	0.013	0.09	T3<T1	-4.774	**$5e^{-6}$**
Treatment x Site	4	95	0.756	0.438	T3=T5	4.196	**0.001**
Plot (Treatment x Site)	30	126	0.342	**0.001**	T4<T1	21.99	**$<2e^{-16}$**
Error	80	368			T4=T5	0.885	0.019
ERA					T2=T1	0.859	0.395
Treatment	4	4292.1	14.187	**0.013**	T2>T5	4.878	**$1e^{-5}$**
Site	1	64.5	0.346	0.44	T3<T1	1.369	0.178
Treatment x Site	4	1210.2	1.621	0.195	T3=T5	-6.284	0.99
Plot (Treatment x Site)	30	5599.7	1.062	0.404	T4<T1	-4.402	**$6e^{-5}$**
Error	80	14066.7			T4=T5	-2.553	0.98
Filamentous algae					T2=T1	3.964	**0.002**
Treatment	4	205.03	9.585	0.353	T2<T5	1.523	0.06
Site	1	320.13	14.966	2e-5	T3>T1	2.82	**0.003**
Treatment x Site	4	136.99	6.404	1e-5	T3=T5	-3.090	**0.003**
Plot (Treatment x Site)	30	12.56	0.587	0.06	T4>T1	-3.017	**0.002**
Error	80	21.39			T4=T5	2.76	**0.008**
Sessile invertebrates					T2=T1	2.144	0.04
Treatment	4	665.3	9.843	**0.02**	T2<T5	3	**0.002**
Site	1	0.1	0.007	0.07	T3>T1	3.503	**0.001**

Treatment x Site	4	67.9	0.835	0.486	T3=T5	-1.607	0.115
Plot (Treatment x Site)	30	108.9	0.84	0.301	T4>T1	-5.239	**$1e^{-6}$**
Error	80	82.855			T4=T5	-0.829	0.411
Foliose red algae [log(y+0.001)]					T2=T1	2.569	0.02
Treatment	4	57.97	0.98	0.493	T2<T5	-8.477	**$5e^{-11}$**
Site	1	205.87	36.684	**$1e^{-6}$**	T3>T1	3.87	**$3e^{-5}$**
Treatment x Site	4	59.17	10.54	**$1e^{-5}$**	T3=T5	0.358	0.131
Plot (Treatment x Site)	30	5.61	0.358	**0.001**	T4>T1	-3.695	**0.001**
Error	80	15.7			T4=T5	0.358	0.448
Juvenile brown canopy algae [log(y+0.001)]					T2=T1	0.915	0.365
Treatment	4	402.55	428.954	**1e-5**	T2<T5	-17.87	**$<2e^{-16}$**
Site	1	4.84	3.797	0.07	T3>T1	-18.03	**$<2e^{-16}$**
Treatment x Site	4	0.94	0.736	0.45	T3=T5	3.885	**0.001**
Plot (Treatment x Site)	30	1.25	0.853	0.31	T4>T1	-4.201	**0.001**
Error	80	1.5			T4=T5	-3.847	**0.001**
Understorey foliose brown algae [(log y+0.001)]					T2=T1	-1.607	0.115
Treatment	4	193.84	11.464	**0.05**	T2<T5	2.5	**0.001**
Site	1	6.07	0.36	0.464	T3>T1	2.985	**0.002**
Treatment x Site	4	32.66	1.93	0.106	T3=T5	-3.356	**0.001**
Plot (Treatment x Site)	30	15.54	0.919	0.41	T4>T1	-5.933	**$1e^{-7}$**
Error	80	16.91			T4=T5	1.149	0.257

Overstorey algae

Throughout the experiment, in the treatment patches where only *C. rodgersii* was removed there was an increase in the density and cover of all overstorey algae, excluding *Cystophora* spp. (Figures 10, 11, Table 8, 9). After 13 months, there was higher density but lower cover of total overstorey algae and the main components of the canopy (*Ecklonia radiata, Phyllospora comsa*) in the treatment patches compared with the intact algal patches (Figures 10, 11, Table 8, 9). The density and cover of total overstorey algae and of *E. radiata, p. comsa, Sargassum* spp. and other canopy forming spp. were also significantly higher in the treatment patches than in the unmanipulated *C. rodgersii* barrens patches (Figures 10, 11, Table 8, 9). There were no detectable differences in the density and cover of *Cystophora* spp. between the treatment patches where *C. rodgersii* and all regrowth was removed, and the unmanipulated *C. rodgersii* barrens patches (Figures 10, 11, Table 8, 9). These trends were consistent between patches of the same treatment within site, however there were higher densities of *P. comsa* and higher cover of total overstorey algae, *E. radiata* and *P. comsa* at site A than at site B, suggesting differential recruitment potential at the two sites (Figures 10, 11, Table 8, 9). Our removals of *C. rodgersii* and canopy algae regrowth were effective in maintaining a low density and cover of overstorey algae throughout the experiment (Figures 10, 11, Table 8, 9). After 13 months, the density and cover of total overstorey algae, *Cystophora* spp., *E. radiata*, *P. comsa* and *Sargassum* spp. other canopy algae, in the treatment patches and in the unmanipulated *C. rodgersii* barrens patches were similar (Figures 10, 11, Table 8, 9). The density and cover of total overstorey algae, *Cystophora* spp., *E. radiata*, *P. comsa* and *Sargassum* spp., and other canopy-forming species in this treatment was also significantly lower than in the patches in the intact algal beds (Figures 10, 11, Table 8, 9).

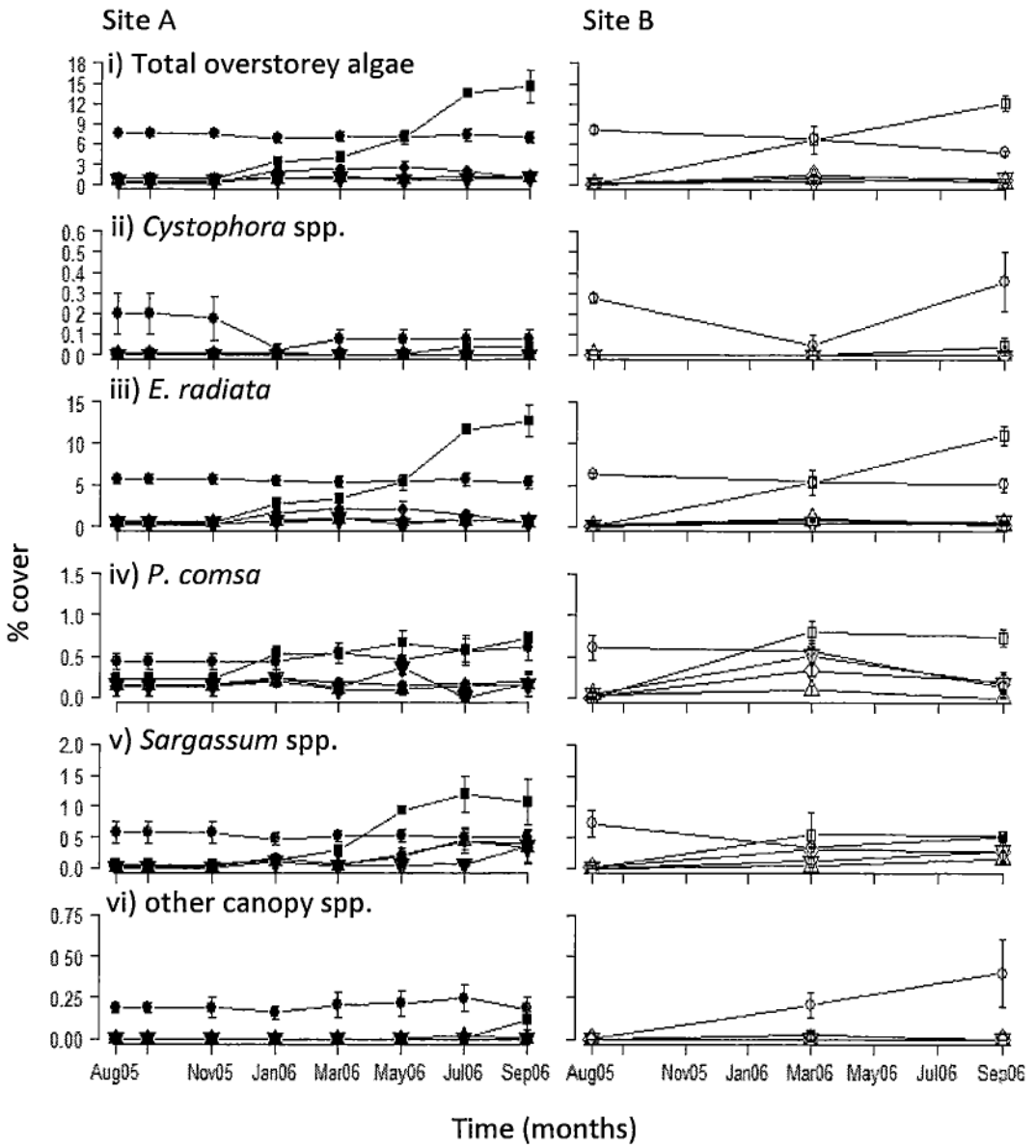

Figure 10. Mean stipes density (+/-SE) of (i) total overstorey algae, (ii) *Cystophora* spp., (iii) *E. radiata,* (iv) *P. comsa,* (v) *Sargassum* spp., and (vi) other canopy spp. through time, at the Lanterns. Treatments are, upright triangles=unmanipulated *C. rodgersii* barrens patches, diamonds=removals of *C. rodgersii* and all regrowth from patches, downward triangles=removals of both *C. rodgersii* and canopy algae regrowth from patches, squares=removals of only *C. rodgersii* from patches, circles=control no *C. rodgersii* in intact algal patches, n=3 replicates for each (see Table 8 for ANOVA results).

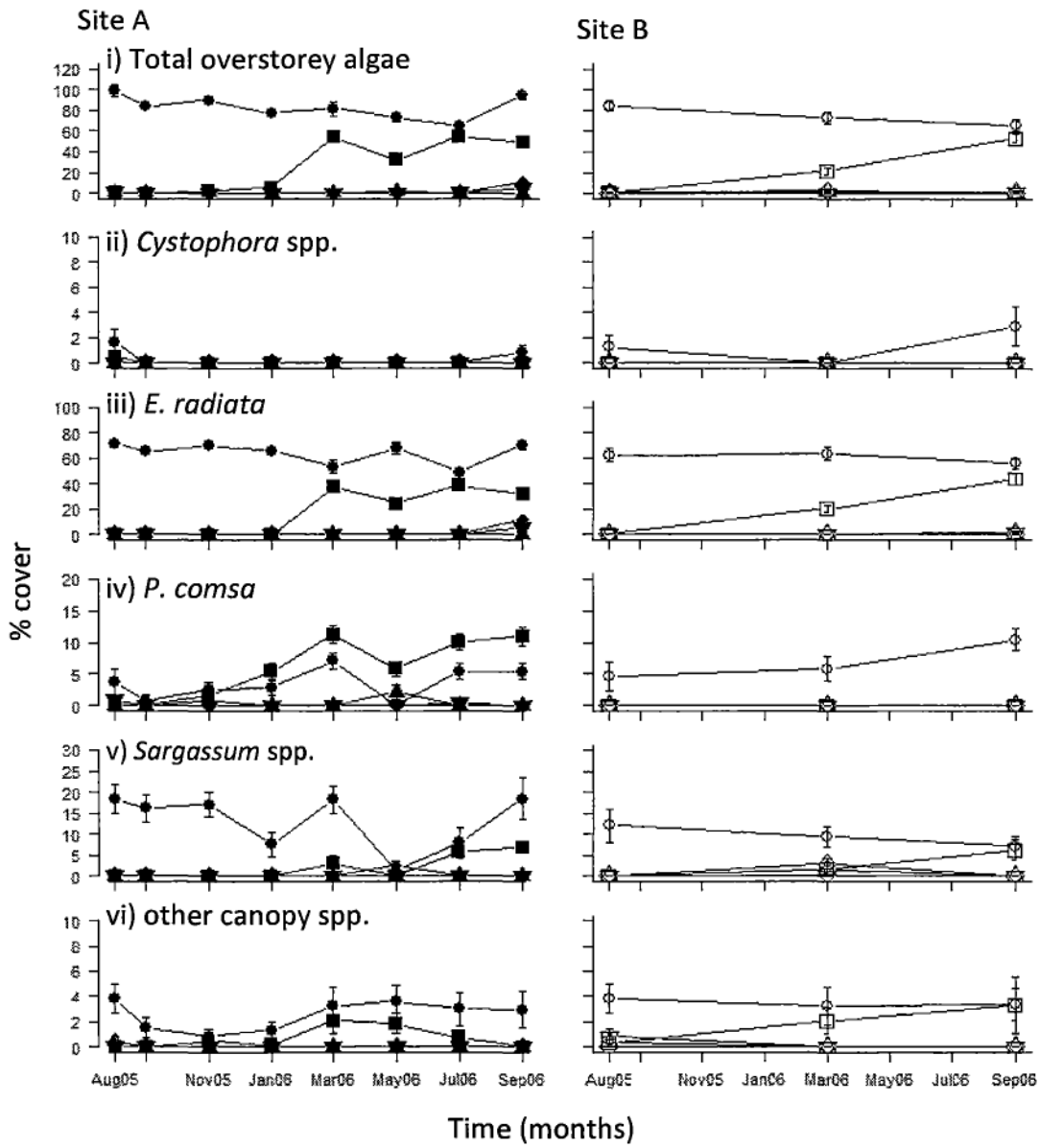

Figure 11. Mean stipes density (+/-SE) of (i) total overstorey algae, (ii) *Cystophora* spp., (iii) *E. radiata,* (iv) *P. comsa,* (v) *Sargassum* spp., and (vi) other canopy spp. through time, at the Lanterns. Treatments are, upright triangles=unmanipulated *C. rodgersii* barrens patches, diamonds=removals of *C. rodgersii* and all regrowth from patches, downward triangles=removals of both *C. rodgersii* and canopy algae regrowth from patches, squares=removals of only *C. rodgersii* from patches, circles=control no *C. rodgersii* in intact algal patches, n=3 replicates for each (see Table 8 for ANOVA results).

Table 8. Overstorey algae. Results of 2-way ANOVAs and planned comparisons testing the effect of experimental manipulations on the density of stipes of total overstorey algae, *Cystophera* spp., *E. radiata, P. comsa*, other brown spp., and *Sargassum* spp in patches. Significant p-values are shown in bold print: $p<0.05$ are significant for the main analysis and $p<0.0125$, are significant for the planned comparisons (α adjusted using Todd and Keough (1994)).

Factors	**df**	**MS**	***F***	**p**	**Comparisons**	***T***	**p**
Total overstorey algae					T2=T1	0.351	0.733
Treatment	4	0.34	6.384	**0.05**	T2<T5	14.698	**$2e^{-8}$**
Site	1	0.114	1.816	0.29	T3≠T1	2.015	0.035
Treatment x Site	4	0.063	1.656	0.2	T3<T5	-4.714	**0.004**
Error	20	0.038			T4>T1	-9.671	**$1e^{-6}$**
					T4=T1	-4.288	**$1e^{-4}$**
***Cystophera* spp.**					T2=T1	0.451	0.877
Treatment	4	0.007	3355.915	**$2e^{-7}$**	T2<T5	2.781	**0.005**
Site	1	0.001	1	0.5	T3≠T1	0.352	0.743
Treatment x Site	4	0.001	0.001	**$2e^{-6}$**	T3<T5	-2.781	**0.005**
Error	20	0.002			T4>T1	-1.58	0.05
					T4=T1	8.125	**0.001**
E. radiata					T2=T1	-1.398	0.192
Treatment	4	149.97	102.562	**0.002**	T2<T5	13.464	**$5e^{-8}$**
Site	1	0.1	0.065	**0.012**	T3≠T1	1.491	0.167
Treatment x Site	4	1.46	0.068	0.397	T3<T5	-7.308	**$1e^{-5}$**
Error	20	2.1			T4>T1	-10.47	**$5e^{-7}$**
					T4=T1	-5.271	**0.004**
P. comsa					T2=T1	0.611	0.581
Treatment	4	0.166	2.927	**0.01**	T2<T5	2.257	**0.01**
Site	1	0.186	3.29	0.138	T3≠T1	-0.556	0.59

Treatment x Site	4	0.057	0.529	0.284	T3<T5	-8.442	**$4e^{-6}$**
Error	20	0.107			T4>T1	2.815	**0.005**
					T4=T1	-0.188	0.854
Other canopy spp. [asin(sqrt(y/100)]					T2=T1	1.13	0.285
Treatment	4	0.001	62425.12	**$8e^{-10}$**	T2<T5	2.981	**0.009**
Site	1	2e-8	1	0.5	T3≠T1	0.927	0.15
Treatment x Site	4	2e-8	9e-5	**$2e^{-8}$**	T3<T5	4.791	**0.004**
Error	20	0.002			T4>T1	-6.151	**$1e^{-9}$**
					T4=T1	-2.562	0.03
***Sargassum* spp. [ain(sqrt(y/100)]**					T2=T1	1.23	0.321
Treatment	4	0.002	8.448	**0.03**	T2<T5	8.272	**$4e^{-6}$**
Site	1	0.002	1	0.5	T3≠T1	0.581	0.705
Treatment x Site	4	0.002	2.419	0.08	T3<T5	-8.272	**$4e^{-6}$**
Error	20	0.0001			T4>T1	-1.581	0.145
					T4=T1	2.732	**0.011**

Table 9. Overstorey algae. Results of 2-way ANOVAs and planned comparisons testing the effect of experimental manipulations on the cover of total overstorey algae, *Cystophera* spp., *E. radiata, P. comsa*, other brown spp., and *Sargassum* spp. Significant p-values are shown in bold print: $p<0.05$ are significant for the main analysis and $p<0.0125$, are significant for the planned comparisons (α adjusted using Todd and Keough (1994)).

Factors	**df**	**MS**	***F***	**p**	**Comparisons**	***T***	**p**
Total overstorey algae [log(y+0.001)]	4	599.66	5.818	**0.05**	T2=T1	0.311	0.99
Treatment	1	153.95	110.108	**$1e^{-11}$**	T2<T5	16.2	**$<2e^{-16}$**
Site	4	103.07	73.714	**$4e^{-15}$**	T3≠T1	1.666	0.06
Treatment x Site	30	1.4	0.311	**3e-4**	T3<T5	16.2	**$<2e^{-16}$**
Plot (Treatment x Site)	80	4.5			T4>T1	-25.19	**$<2e^{-16}$**
Error					T4=T1	5.241	**$4e^{-6}$**
***Cystophera* spp. [asin(sqrt(y/100)]**	4	0.019	1.67	0.117	T2=T1	0.632	0.754
Treatment	1	0.003	0.302	0.16	T2<T5	2.388	**0.01**
Site	4	0.003	15.915	**$4e^{-7}$**	T3≠T1	0.523	0.498
Treatment x Site	30	0.002	0.169	**3e-7**	T3<T5	-2.388	**0.01**
Plot (Treatment x Site)	80	0.004			T4>T1	0.581	0.564
Error					T4=T1	2.388	**0.01**
E. radiata					T2=T1	0.626	0.25
Treatment	4	18145	27.046	**0.004**	T2<T5	17.416	**$<2e^{-16}$**
Site	1	367	5.111	**0.04**	T3≠T1	1.576	0.122
Treatment x Site	4	671	9.332	**$5e^{-5}$**	T3<T5	-18.58	**$<2e^{-16}$**
Plot (Treatment x Site)	30	72	0.776	0.221	T4>T1	-11.36	**$3e^{-15}$**
Error	80	93			T4=T1	5.717	**$8e^{-7}$**
***P. comsa* [asin(sqrt(y/100)]**					T2=T1	0.626	0.25
Treatment	4	0.438	12.218	**0.016**	T2<T5	5.154	**$2e^{-6}$**

Site	1	0.085	50.591	**$6e^{-8}$**	T3≠T1	0.626	0.25
Treatment x Site	4	0.036	21.481	**$2e^{-8}$**	T3<T5	-5.154	**$2e^{-6}$**
Plot (Treatment x Site)	30	0.002	0.072	**$6e^{-12}$**	T4>T1	-6.593	**$1e^{-8}$**
Error	80	0.024			T4=T1	0.581	0.564
Other canopy spp. [asin(sqrt(y/100)]					T2=T1	0.877	0.987
Treatment	4	0.329	62.065	0.266	T2<T5	8.364	**$4e^{-11}$**
Site	1	0.053	9.924	**$3e^{-5}$**	T3≠T1	0.877	0.987
Treatment x Site	4	0.168	31.698	**$2e^{-15}$**	T3<T5	-0.887	**$4e^{-11}$**
Plot (Treatment x Site)	30	0.002	0.4	**0.003**	T4>T1	-4.522	**$2e^{-5}$**
Error	80	0.006			T4=T1	1.832	0.08
***Sargassum* spp. [asin(sqrt(y/100)]**					T2=T1	0.877	0.987
Treatment	4	0.041	2.2	0.232	T2<T5	2.629	**0.005**
Site	1	0.012	1.675	0.206	T3≠T1	-1.272	0.21
Treatment x Site	4	0.007	2.723	**0.05**	T3<T5	-2.629	**0.005**
Plot (Treatment x Site)	30	0.009	0.847	0.311	T4>T1	-2.418	**0.005**
Error	80				T4=T1	0.589	0.495

DISCUSSION

Global climate change is leading the redistribution of non-indigenous species with the potential to alter ecosystems structure and function (e.g. Parmesan & Yorke 2003, Harley et al. 2006). In its new range in eastern Tasmania, the long spined urchin, *Centrostephanus rodgersii,* has a major influence negative influence on local biodiversity (Johnson et al. 2005, Ling 2008). We demonstrated that *C. rodgersii* had both direct and indirect impacts on the amount of bare rock, the cover of algae and sessile invertebrates, and the abundances of two commercially fished native herbivores, blacklip abalone (*Haliotis rubra*) and the urchin (*Heliocidaris erythrogramma*). The impacts of *C. rodgersii* varied between species and life stages.

Direct impacts of a range expanding urchin on commercially fished native herbivores

Our field experiment, suggested *C. rodgersii* has a direct negative impact on the abundances of adult and juvenile *H. rubra,* through competition for food. Similar research in New South Wales also showed, experimental removals of *C. rodgersii* from large scale plots resulted in overgrowth of barrens habitat by filamentous and foliose algae and sessile invertebrates and concomitant increases in the densities of juvenile *H. rubra* (Andrew et al. 1998). In other manipulations, introductions of *C. rodgersii* into enclosures in intact algal beds, in Tasmania, resulted in declines in the total weight, dry weight stomach contents and survivorship of adult *H. rubra* relative to controls without *C. rodgersii* (Strain & Johnson 2009, Chapter 3). This research suggests *C. rodgersii* is the superior competitor for food in interactions with both adult and juvenile *H. rubra* (Andrew et al. 1998, Strain & Johnson 2009).

Removal of *C. rodgersii* from treatment patches, irrespective of algal manipulations, invariably resulted in an increase in the density of adult *H. erythrogramma* relative to unmanipulated *C. rodgersii* barrens patches. These results suggest that *C. rodgersii* has a direct negative impact on the densities of adult *H. erythrogramma,* through competition for shelter in crevices. Studies on other species of urchins have demonstrated that *Diadematidae* can aggressively defend their crevices from both conspecifics and competitors (Williams 1977, McClanahan 1988, Shulman 1990). Our research suggests that *C. rodgersii* is the superior competitor for shelter in

crevices in interactions with *H. erythrogramma.* However, *C. rodgersii* is unlikely to locally exclude the native urchin because its larger test and longer spines prevent it from occupying smaller crevices inhabited by *H. erythrogramma.*

The direct impacts of *C. rodgersii* on *H. rubra* and *H. erythrogramma* could also provide insights into the interactions between the 2 native herbivores. Interestingly, throughout the experiment in the intact algal patches, there was a very low density of adult and juvenile *H. erythrogramma* and a high density of adult and juvenile *H. rubra.* These results are consistent with broad-scale surveys in eastern Tasmania which showed that the total abundances of *H. erythrogramma* and *H. rubra* were negatively correlated at a range of spatial scales, suggesting negative interactions (Johnson et al. 2005). These results suggest that *H. erythrogramma* and *H. rubra* could compete for resources Shepherd 1973a, Andrew & Underwood 1992, Johnson et al. 2005), or that *H. erythrogramma* prefers habitat that is relatively clear of attached algae.

Indirect impacts of a range expanding urchin on commercially fished native herbivores

Our removals of canopy algae to simulate *C. rodgersii* grazing had an indirect negative effect on the density of adult and juvenile *H. rubra* and adult *H. erythrogramma.* Our results are consistent with other research in Tasmania, which demonstrated removals of canopy algae from large experimental plots, resulted in a decrease in the total abundances of *H. rubra* and *H. erythrogramma* (Edgar et al. 2004). In the reverse of this manipulation, Andrew (1993) found that the densities of juvenile *H. rubra* and *H. coccoradiata* increased after boulders covered in *E. radiata* were transplanted into urchin barrens. (Edgar et al. 2004) The loss of biogenic habitat structure in *C. rodgersii* barrens could increase the risk of predation (Edgar et al. 2004) and decrease the availability of suitable habitat for *H. rubra* and *H. erythrogramma* (Andrew et al. 1998).

While the negative effects of *C. rodgersii H. rubra* and *H. erythrogramma* seem clear, our results also suggest *C. rodgersii* grazing could also benefit juvenile *H. erythrogramma.* Densities of juvenile *H. erythrogramma* were higher in the treatment where *C. rodgersii* and all regrowth were removed than in the treatment where only *C. rodgersii* was removed. *C. rodgersii* barrens habitat could have several advantageous for juvenile *H.*

juvenile *H. erythrogramma* including reduced risk of predation (Garnick 1989, Johnson et al. 2005), decreased physical abrasion by algae (Konar 2000) or an increase suitable habitat for attachment and feeding (Konar 2000). *C. rodgersii* grazing is important in maintain barrens habitat (Fletcher 1987, Johnson et al. 2005, Ling 2008), but that is a dictomy because the densities of juvenile *H. erythrogramma* were lower in unmanipulated *C. rodgersii* barrens patches. Thus, a lower density of *C. rodgersii* could have a positive impact on the densities of juvenile *H. erythrogramma* but as the density increases *C. rodgersii* has a negative impact on the density of juvenile *H. erythrogramma* through competition or predation.

The climate induced range expansion of *C. rodgersii* and formation of urchin barrens will have both direct and indirect negative impacts on the populations of *H. rubra* and *H. erythrogramma* on the east coast of Tasmania (Johnson et al. 2005, Strain & Johnson 2009). We demonstrated that *C. rodgersii* has a major negative impact on the abundances of adult and juvenile *H. rubra* and adult *H. erythrogramma,* through direct competition for food and shelter. In contrast, *C. rodgersii* overgrazing of canopy algae resulted in slight declines in the abundances of adult and juvenile *H. rubra* and adult *H. erythrogramma,* indirectly through loss of biogenic habitat. These results suggest that the effects of the direct interactions between *C. rodgersii* and *H. rubra* and *H. erythrogramma* are stronger than the indirect interactions.

Effect of urchin range expansion on reef habitat

Urchins can have a major influence on benthic habitat (for review: Lawrence 1975, Breen & Mann 1976, Tegner & Dayton 2000). It is already well recognised that *C. rodgersii* grazing has an important influence in structuring temperate rocky reef ecosystems in south-east Australia (Fletcher 1987, Johnson et al. 2005, Ling 2008). In its new habitat on the east coast of Tasmania, this urchin is responsible for overgrazing the algal and sessile invertebrate habitat and maintaining simplistic and homogeneous bare rock benthic habitat (Johnson et al. 2005, Ling 2008). This barrens habitat is similar to the barrens described in its endemic range (Andrew & Underwood 1992) and broadly typically of urchin barrens throughout the world (Pinnegar et al. 2000).

Experimental removals of *C. rodgersii* from barrens patches, resulted in bare rock being overgrown, by filamentous algae (primarily red algae), foliose

algae (red, juvenile canopy-forming and understorey foliose brown algae) and sessile invertebrates. However, after 12 months there were still significant differences in the benthic community structure between patches where only *C. rodgersii* was removed and the patches in intact algal beds. Removal of *C. rodgersii* from barrens patches resulted in a rapid return to an algal dominated state in which cover exceed 50 % at 8-12 months after urchin removal, however recovering patches were biased towards smaller and more abundant canopy forming algae and a lower cover of encrusting red algae, relative to intact algal patches (Ling 2008). Complete recovery of the algal community following the removal of *C. rodgersii* can take many years, and is likely to be a function of the size of the cleared area and its proximity to established reproductive algae (Fletcher 1987, Ling 2008). These results suggest *C. rodgersii* barrens in southeast Australia are an alternative and stable configuration of the benthic habitat (Andrew & Byrne 2001, Ling 2008).

Effect of range expanding urchin on ecosystems structure and function

The range expansion of *C. rodgersii* in southeast Australia will have major impacts the structure and function of the temperate rocky reef ecosystem (Johnson et al. 2005, Ling 2008). The catastrophic shift from productive and diverse algal beds to *C. rodgersii* barrens is predicted to negatively impact on 100's of taxa, including algae, benthic fauna and fishes (Edgar 1997, Graham 2004, Ling 2008). The loss of these taxa is likely to impact on many abiotic and biotic processes (Graham 2004, Ling 2008) Thus, the formation of extensive *C. rodgersii* barrens is predicted to reduce both primary (Chapman 1981, Babcock et al. 1999) and secondary productivity (Duggins et al. 1989) with flow on effects to many other species (Andrew & Underwood 1992, Andrew et al. 1998, Johnson et al. 2005, Ling 2008, Strain & Johnson 2009, Chapter 2, 3).

Effects of range expanding generalist grazers on ecosystems

Climate change is predicted to alter the range of many non-indigenous species (Parmesan 1996, Hickling et al. 2006). Many of these non-indigenous species are not highly invasive and are unlikely to have major impacts on ecosystems (Bruno et al. 2005). Many highly invasive species are generalist grazers (e.g. gastropods, urchins, limpets and periwinkles), that can have major negative impacts on native biota, both in their endemic range and new habitat (Carlton 1992, Carlton & Geller 1993, Ruiz et al. 1999, Byers 2000, Grosholz 2002, Nunez et al. 2010). These results strongly suggest that generalist grazers can have disproportionate impact on

ecosystems structure and function (Carlton & Geller 1993, Ruiz et al. 1999, Byers 2002, Johnson 2007, Nunez et al. 2010).

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CHAPTER 5: SCALE-DEPENDENT RELATIONSHIPS BETWEEN BENTHIC HABITAT CHARACTERISTICS AND ABUNDANCES OF BLACKLIP ABALONE, *HALIOTIS RUBRA* (LEACH).

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ABSTRACT

Habitat characteristics can influence the density and size of marine herbivores at a range of spatial scales. We examined the relationship between benthic habitat characteristics and adult blacklip abalone (*Haliotis rubra*) densities across local scales (0.0625-16m^2), at 2 depths, 4 sites and 2 locations on the east coast of Tasmania, Australia. Biotic characteristics that were important in explaining abalone densities included cover of non-calcareous encrusting red algae (NERA), non-geniculate coralline algae (NCA), a matrix of filamentous algae and sediment, sessile invertebrates, and foliose red algae. The precision of relationships between these characteristics and abalone densities varied with spatial scale. At smaller scales (0.0625-0.25 m^2), there was a positive relationship between NERA and *H. rubra* densities and negative relationships between sediment matrix, sessile invertebrates and abalone densities. At the largest scale (16 m^2), there was also a positive relationship between NERA and abalone densities. Thus, for some biotic characteristics, small-scale spatial relationships are scalable. There was very little variation in these patterns between depths, sites or locations. Our results could be explained by a dynamic interplay between the behavioural responses of *H. rubra* to microhabitat, and/or to abalone being directly involved in maintaining NERA free of algae, sediment, and sessile invertebrates.

Keywords: quantile regression, generalized linear modeling, BEST, percentage cover, scale-dependent, *H. rubra*

INTRODUCTION

Benthic habitat characteristics can influence the density and size of marine herbivores however, the nature of the relationship is usually dependent on the spatial scale of observation (Anderson 2004, Benedetti-Cecchi et al. 2001, Fowler-Walker & Connell 2002, Menconi et al. 1999, Terlizzi et al. 2007, Underwood & Chapman 1996). At some spatial scales, the association between benthic habitat characteristics and marine herbivores abundance is clear, while at others relationships may be confused or non-existant (Syms 1995). Identifying the spatial scales at which the relationship between benthic habitat characteristics and marine herbivore abundance are clearest is important, because it helps to formulate hypotheses about the way herbivores respond to and influence benthic habitat characteristics, and determines the extent which, processes are scaleable. These are important considerations in assessing the reliability of the relationship between habitat features and herbivore abundances, and by inference the underlying predictions of anthropogenic impacts on marine ecosystems (Bishop et al. 2002). In practice, understanding patterns and underlying processes at multiple spatial scales represents a major challenge for ecologists (Syms 1995).

Blacklip abalone (*Haliotis rubra*) is a commercially important macro-invertebrate found abundantly across a wide range of habitats and wave exposures in south-east Australia (Shepherd 1973). Understanding the effects of benthic habitat characteristics on *H. rubra,* and how abalone might influence benthic habitat characteristics, is important for predicting and managing the distribution of local populations across a range of different habitats types. Important abiotic factors are likely to include the abundances of different types of substrata (Shepherd 1973, Nash et al. 1995). Biotic factors are likely to be cover of non-calcareous encrusting red algae (NERA), non-geniculate coralline algae (NCA) (Nash et al. 1995, Daume et al. 1999, Valentine et al. 2008), the amount and type of overstorey and understorey algae (Shepherd 1973, Valentine et al. 2008), and the cover of sessile invertebrates (Valentine et al. 2008). However, associations of abalone with these groups are typically based on casual observation rather than quantitative studies (but see Dixon et al. 1998, Shepherd 1973).

The relationships between benthic habitat characteristics and the density and size of *H. rubra* are likely to be influenced by the spatial scale of observation. Broad-scale surveys (50 m^2) on the east coast of Tasmania demonstrated weak positive correlations between the cover of encrusting red

algae (ERA, combined NERA and NCA) and densities of *H. rubra,* and weak negative correlations between the cover of sessile invertebrates and understorey algae and the densities of abalone (Valentine et al. 2008). In contrast, surveys at smaller spatial scales showed a strong positive association between the cover of ERA and densities of *H. rubra* (Valentine & Mundy unpublished data). These results suggest the relationships between benthic habitat characteristics on *H. rubra* are clearest at smaller spatial scales. The current research focused primarily on the 6 to 8 m depth range and exposed coastlines. A comparison of the relationship between benthic habitat characteristics and abalone density and mean size at different locations, depths, sites and quadrat sizes is of interest to provide a framework for formulating hypotheses about small-scale processes that influence the distribution of *H. rubra.*

Testing the relationship between the habitat characteristics and the densities and size of marine species is methodologically complex and typically involves multiple steps. Initially, there are multiple habitat characteristics and it is important to determine which factor(s) have the most influence on the densities and size of marine species. Once the common habitat characteristics have been identified, the relationship between the habitat characteristics and the abundance and size of marine species needs to be described (Vaz et al. 2008). Many habitat and species relationship take the form of a polygon in which the upper boundary describes how their abundance or size is limited by the factor of interest, while variation below this boundary reflects the limiting effect of a myriad of other environmental attributes other than the factor of interest on abundance or size of the species (Cade et al. 1999, Vaz et al. 2008). Specific techniques are required to analyse these so-called 'factor ceiling' relationships because the data is highly variable and zero inflated (Cade et al. 1999). We outline a specific approach using multiple models that will best capture all aspects of the relationship between biotic habitat characteristics and the densities and size of *H. rubra.*

In this study we used three models to estimate the nature of the relationship between benthic characteristics on the density and size of *H. rubra.* The objectives of the study were to (1) identify the benthic habitat characteristics that best predict densities and size of *H. rubra,* (2) describe the relationship between these habitat characteristics and densities and size of *H. rubra* at different spatial scales, (3) identify the spatial scale(s) at which those

relationships are most clear, and (4) assess variability across different sites, depths and locations in the nature of these relationships.

MATERIALS AND METHODS

Study site characteristics

Surveys were conducted at two locations on the east coast of Tasmania, George Third Rock research area and Maria Island marine reserve (Figure 1). Four sites (separated by at least 100 m) were selected randomly within each location. At each site, sampling was undertaken in shallow (1 to 3 m Maria Island and 3 to 6 m George Third Rock) and deep (7 to 9 m Maria Island and 16 to 19 m George Third Rock) water, where previous research showed that there are locally high densities of blacklip abalone (*Haliotis rubra*) (Prince 1989, Edgar & Barrett 1999).

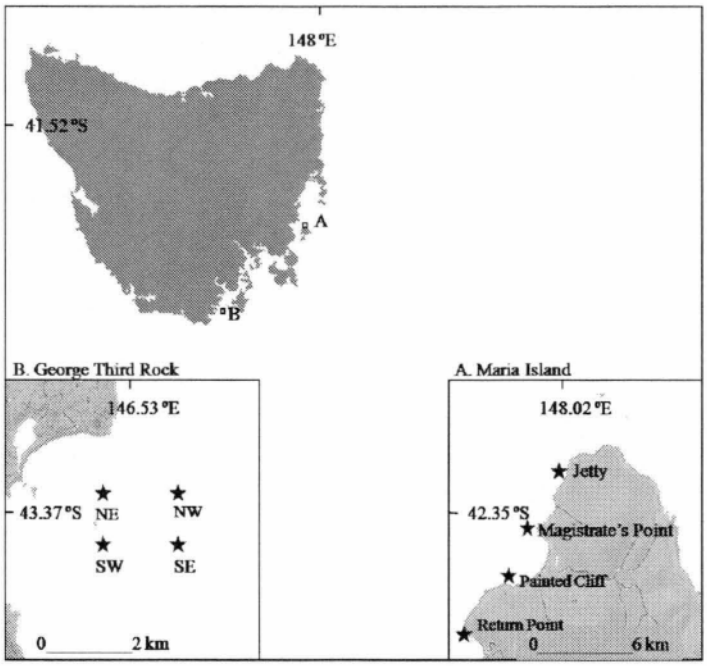

Figure 1. Map of the east coast of Tasmania, Australia, showing the study locations, George Third Rock and Maria Island and the 4 study sites within each region.

The sites at George Third Rock (northeast, northwest, southeast and southwest) are characterized by gently sloping rocky substratum to a depth of 19 m, with moderate topographic relief. This location is exposed to southeasterly swells and classified as moderately exposed with a diverse algal assemblage (Edgar 1984). The understorey community consists of foliose red algae, non-calcareous encrusting red algae (NERA) and non-geniculate coralline algae (NCA), filamentous algae, foliose algae, a matrix of sediment and filamentous algae, and sessile invertebrates. There is a dense overstorey of large brown seaweeds, largely comprising of *Phyllospora comosa* (Labillardiere), *Ecklonia radiata* (C.agardh) and *Xiphophora gladiata* (Labillardiere).

The sites at Maria Island (the Jetty at Darlington Habour, Magistrate's Point, Painted Cliffs and Return Point) are characterized by gently sloping rocky substratum to a depth of 11 m with moderate topographic relief. All sites are exposed to the southwest but are classified as sheltered with a diverse algal assemblage (Edgar 1984). Overstorey algal species include *Cystophera retroflexa* (Labillardiere), *E. radiata* and *Sargassum fallax* (Sonder). The understorey community consists of a rich variety of foliose algae (mostly red algae), filamentous algae, NERA, NCA, the sediment matrix, and sessile invertebrates.

Sampling design

At each depth and site, two SCUBA divers sampled 12 replicate quadrats, which were divided into five sizes, *viz.* 0.25x0.25 m, 0.5x0.5 m, 1x1 m, 2x2 m, and 4x4 m. All quadrats were located randomly (on the basis of randomly determined fin kicks and compass bearings). The percentage cover of the benthic habitat characteristics (ES) and the number and size of grazers (BC and MD) were consistently assessed by the same divers. All divers possessed considerable experience (>100 h) in underwater visual quadrat work.

In each quadrat size, the abundance of *H. rubra* and other grazers were counted, and the maximum shell length of all *H. rubra* were measured using vernier calipers. The counts of *H, rubra* and other grazers were converted to densities (per m^2). At George Third Rock *H. rubra* shell length ranged from 36 -199 mm, while at Maria Island lengths varied from 57-203 mm.

The percentage cover of the various benthic habitat characteristics were obtained by visual estimation. In this method, points were marked along the edges of each quadrat size and the percentage cover of each habitat characteristics was determined by counting the number of small squares each habitat characteristic covered. The method enables benthic habitat characteristics to be estimated to the nearest 5%. Because the differences in the percentage cover between quadrats, were a lot greater than 5% this precision was sufficient to conduct the analyses. To assess the reliability the method we undertook a pilot trial, in which we compared the results from visual estimation, as just described, to those assessed using the points intercept method (n=12 quadrats). There was no significant difference in accuracy or precision, irrespective of quadrat size.

For each quadrat size, we initially assessed the percentage cover of the overstorey algal species. The fronds of these algae were then moved aside to allow assessment of the percentage cover of the understorey community. Note that, given multiple layers (e.g. overstorey overlaying understorey algae), the total cover of algae for any given quadrat size could exceed 100%. All overstorey algae were identified to species while the understorey community was identified to broader guilds of algae and invertebrates (e.g. foliose red algae, ascidian, bryozoan, sponge, etc). The percentage cover of different substratum types was then classified as either flat rock (>5 m diameter), very large boulders (>2.5 m to <5 m diameter), large boulders (>1 m to <2.5 m diameter), small boulders (>0.2 m to <1 m diameter), cobbles (>0.1 m to <0.2 m diameter), pebbles (>0.01 m to <0.1 m diameter), gravel (<0.01 m diameter) or sand.

Analysis

Because the two locations sampled (George Third Rock and Maria Island) have different exposures, depths and algal communities, we conducted analyses separately for each location. We also conducted all analyses separately for each quadrat size. Rare taxa (found in <2 quadrat sizes) were excluded from the analyses.

We used three different techniques, BEST (Primer 6.0), generalized liner modelling (GLM) and quantile regression (Cade et al. 1999) to quantify the relationship between benthic habitat characteristics and the densities and size of *H. rubra*. For each quadrat size, we began by using BEST to identify a reduced number of habitat characteristics that were best correlated with *H.*

rubra density and size. We then used individual GLMs to assess which of the highly correlated characteristics (identified by BEST) explained the most variability in the density and size of *H. rubra,* for each quadrat size. We used quantile regression models to determine the optimal quadrat size(s) for measuring the relationship between the common habitat characteristics and *H. rubra* density and size. Initially data for the BEST, GLM and quantile regression analyses were pooled across depth and site. For those quadrat size(s) in which relationships were most clearly defined, we used quantile regression to test the effects of depth and site on the relationship between the habitat characteristics and the density and mean size of *H. rubra.* We used quantile regression to test the relationship between the habitat characteristics, and the densities and mean size of *H. rubra,* for each quadrat size because this technique is ideal for dealing with responses that exhibit a heterogeneous variance in relation to predictor variables and zero-inflated data (Cade et al. 1999)

Correlation between habitat characteristics and *H. rubra*

The BEST approach was used to identify the habitat characteristics (single variables and guilds) that best correlated with the density and average shell length of *H. rubra,* in each quadrat size. Bray-Curtis similarity matrices were calculated for all data after a square root transformation to reduce the influence of dominant observations. We calculated that BEST models could be run using no more than 20 common predictor variables (those found in ≥ 3 quadrat sizes) to protect against over-definition.

Variance explained by habitat characteristics in *H. rubra*

For each quadrat size, we used GLMs to assess which of the highly correlated habitat characteristics (identified using BEST) explained the most variability in the density and average shell length of *H. rubra.* As the data consisted of counts, a log-link function was used with a Poisson or quasi-Poisson distribution. GLMs were undertaken using the R statistical package.

Pair-wise correlations of all abiotic and biotic habitat characteristics were calculated and checked to ensure that the variables included in the generalized linear models were not highly correlated. Because the abiotic factors were highly correlated with each other and with the biotic factors, only the individual biotic factors were included in the GLMs. Predictor values were first normalized to z-scores to allow direct comparisons of parameter coefficients in the fitted models.

Effect of quadrat size on the relationships between the habitat characteristics and *H. rubra*

For each quadrat size, the relationship between the cover of habitat characteristics and average density and shell length of *H. rubra* were analysed individually using linear quantile regression. Quantile regressions are based on a weighted absolute deviance model. They provide a robust estimate of location, are resistant to outliers, and provide an efficient estimator when the residuals are non-normal (Koenker & Machado 1999). The choice of quantiles for the analysis provides estimates of the upper bounds for scattered distributions (Koenker & Machado 1999). Here we examined the upper 70^{th}, 80^{th} and 90^{th} quantiles. We tested the difference between these quantiles using Wald's tests. All quantile regression coefficients and confidence intervals were estimated using R.

The strength of the relationship between the habitat characteristics and the density and average shell length of *H. rubra* were compared (for each quadrat size) using ΔAIC and the coefficient of determination (R^{-1}). ΔAIC was calculated as the difference between the full model and the reduced model (that is the model without the habitat characteristic) (Cade & Guo 2000). R^{-1} was calculated as 1-(Sum (f)/Sum (r)), where Sum (f) is the sum of the weighed absolute deviations minimized in estimating the full model, and Sum (r) is the equivalent metric in the reduced model (Koenker & Machado 1999). We defined the optimal scale(s) to observe the relationship between the habitat characteristic and density or mean size of *H. rubra,* as the quadrat size(s) with high R^{-1} and ΔAIC values.

Effect of depth and site on the relationships between the habitat characteristics and *H. rubra*

Data were insufficient to test the combined effects of depth and site on the relationship between the habitat characteristics and the densities and size of *H. rubra.* Therefore, at the identified optimum quadrat size(s), we used quantile regression to the test how the relationships between the cover of the habitat characteristics and density and average shell length of *H. rubra* varies with depth and site, separately. The model included the main effects of depth (fixed, 2 levels) and site (fixed, 4 levels). Where significant differences were found across sites and/or depths, the relationship between the cover of the habitat characteristics and the densities and average size of *H. rubra* was analysed separately.

RESULTS

Fifty abiotic and biotic factors (as single variables or collectively as guilds) were used to describe the benthic community structure at George Third Rock and Maria Island (Table 1). There were no detectable relationships between the habitat characteristics and average size (shell length) of *H. rubra.* Since there were very few juvenile *H. rubra* (<70 mm shell length) observed at either location, (George Third Rock 5%, and Maria Island 2% of total abalone), the results presented hereafter focus wholly on the relationships between the habitat characteristics and densities of adult *H. rubra.* We also tested and found that there were no detectable relationships between either the abiotic or biotic habitat characteristics and the densities of other grazers, namely the urchins *Heliocidaris erythrogramma* (Valenciennes) and *Centrostephanus rodgersii* (Agassiz) and other chitons, gastropods and limpets.

Table 1, Abiotic and biotic factors (single variables and guilds) recorded in quadrat sizes 0.0625 m^2 to 16 m^2 at George Third Rock and Maria Island. Taxa found only at George Third Rock are indicated by (GIII).

Abiotic variables	**Biotic variables**	**Biotic groups**
Flat rock	Non-calcareous encrusting red algae (NERA)	Encrusting red algae (ERA)
Very large boulder	Non-geniculate coralline algae (NCA)	
Large boulder	Filamentous green algae	Filamentous algae
Small boulder	Filamentous brown algae	
Bare rock	Filamentous red algae	
Cobbles	Filamentous algae/ sediment matrix	Sediment matrix and sessile invertebrates combined
Pebbles	Ascidian	Sessile invertebrates
Gravel	Bryozoan	
Sand	Sponge	
	Branching coralline algae	
	Foliose red algae	
	Caulerpa flexis	Foliose green algae
	Caulerpa geminata	

	Caulerpa trifaria	
	Caulerpa remotifolia	
	Other *Caulerpa* spp.	
	Other green algae	
	Carpoglossum confluens	Understorey foliose brown algae
	Caulocystis cephalornithos	
	Caulocystis wifera	
	Halopteris paniculata (GIII)	
	Perithalia caudata (GIII)	
	Undaria pinnatifida	
	Zonaria spp.	
	Lobophora spp.	
	Other understorey brown algae	
	Cystophera spp.	Overstorey brown algae
	Duvillaea potatorum (GIII)	
	Ecklonia radiata	
	Phyllospora comosa	
	Macrocystis angustifolia (GIII)	
	Lessonia corrugata (GIII)	
	Sargassum spp.	
	Xiphophora gladiata (GIII)	
	Other overstorey algae	

Relationships between habitat characteristics and *H. rubra*

Non-parametric correlations

For each quadrat size, we used the BEST approach to identify which of the 20 habitat characteristics were most highly correlated with the densities of adult *H. rubra* (Appendices 1, 2). For both locations, the habitat characteristics that were consistently selected across the range of quadrat sizes among the 10 best individual and the five combined habitat characteristics included, the cover of non-calcareous encrusting red algae (NERA), non-geniculate coralline algae (NCA), encrusting red algae (ERA, combined ERA and NCA), foliose red algae, sessile invertebrates, the sediment matrix, sessile invertebrates and the sediment matrix combined, and foliose red algae (Appendix 1, 2). At George Third Rock the cover of small boulders was among those variables best correlated with densities of adult *H. rubra,* while at Maria Island the cover of overstorey brown algae featured in correlations with adult abalone densities.

Variation in the relationship between the benthic habitat characteristics and *H. rubra*

For each quadrat size, we used individual generalized linear models (GLMs) to estimate the percentage variance explained in the densities of adult *H. rubra* by the ten habitat characteristics identified using the BEST approach (Table 2). At both locations, and in all quadrat sizes, the cover of NERA explained a large amount of variation in the densities of adult *H. rubra.* At George Third Rock, the cover of the sediment matrix was also important in explaining the variation in the densities of adult *H. rubra* in the smallest (0.25x0.25 m) and largest (4x4 m) quadrat sizes. In contrast, at Maria Island, the cover of the sediment matrix explained a large amount of the variation in the densities of adult *H. rubra* only in the smaller quadrat sizes (0.25x0.25 m, 0.5x0.5 m and 1x1 m). The cover of sessile invertebrates also explained a large amount of the variation in the densities of adult *H. rubra* in all quadrat sizes at George Third Rock, but not at Maria Island. Similarly, in the largest quadrat size (4x4 m), the cover of foliose red algae explained the greatest amount of variation in adult abalone densities at George Third Rock, but not at Maria Island. Cover of NCA and of overstorey brown algae explained very little of the variation in the densities of adult *H. rubra* at either location, irrespective of quadrat size.

Strength of the relationship between the benthic habitat characteristics and *H. rubra*

For each quadrat size we used quantile regression models to describe the relationship between the benthic habitat characteristics (identified by BEST and GLMs) and the densities of adult *H. rubra*. We then compared among the results to identify the optimal quadrat size(s), defined as those with high R^{-1} and ΔAIC values. The optimal quadrat size(s) at which the relationship between the habitat characteristics and the densities of adult *H. rubra* is most clear, depended on the nature of the habitat characteristic in question (Tables 3 and 4).

Table 2. Results of generalized linear multiple regression of the effect of the benthic habitat characteristics on the densities of *H. rubra* at (a) George Third Rock and (b) Maria Island in 0.25x0.25 m, 0.5x0.5, 1x1 m, 2x2 m and 4x4 m quadrat sizes. Values are p-values (p) and the percentage variance (%) explained by individual variables. p≤0.05 are indicated by *, p≤5e-3 ** and p≤5e-4 ***. The largest % variance explained is indicated in boldprint.

Quadrat size	**0.25x0.25 m**		**0.5x0.5 m**		**1x1 m**		**2x2 m**		**4x4 m**	
Variable	**p**	**%**	**p**	**%**	**p**	**%**	**p**	**%**	**p**	**%**
a) George Third Rock										
NERA	***	**62.26**	***	**59.47**	***	**42.48**	***	**23.2**	***	21.52
NCA	***	9.81	***	9.98	***	9	***	1.4	*	6.66
Sediment matrix	***	24.74	***	6.3		0.9	***	3	***	10.73
Sessile invertebrates	***	18.45	***	14.36	***	10.29	***	9.43	***	29.79
Foliose red algae	*	4.65	***	4.06	***	4.3	***	5.56	***	**34.65**
b) Maria Island										
NERA	***	23.32	***	**26.88**	***	**32.35**	***	**17.95**	***	**7.36**
NCA	***	7.62	***	5.01	***	6.77	***	3.3	***	1.37
Sediment matrix	***	**32.78**	***	25.88	***	23.48	***	7	*	0.83
Sessile invertebrates	***	12	**	5.27	*	2.04		0.33		0.62
Foliose red algae		1.28		1.07		0.02		0.09	*	0.94
Overstorey brown algae		0.43		1.87		1.13		0.54		0.63

Table 3. Results of 90th quantile regression analysis testing the relationship between the benthic habitat characteristics and the densities of *H. rubra* at different quadrat sizes (0.25x0.25 m, 0.5x0.5 m, 1x1 m, 2x2 m and 4x4 m) at George Third Rock. Values given are p-values (*p*), and the coefficient of determination (R^{-1}). p≤0.05 are indicated by *, p ≤5e-3 ** and p≤5e-4 *** and the largest values of R^{-1} for each habitat characteristics are indicated in bold-print.

Quadrat size	0.25x0.25 m		0.5x0.5 m		1x1 m		2x2 m		4x4 m	
Variables	**p**	R	**p**	R	**p**	R	**p**	R	**p**	R
NERA	***	0.14	***	**0.18**	**	0.13	**	0.04	***	0.09
NCA	***	0.07	***	**0.08**	**	0.06	**	0.01	*	0.04
ERA	**	**0.23**	**	0.05		0.01		0.01	**	0.12
Sediment matrix	**	**0.43**	*	0.04		0.01		0.02	*	0.01
Sessile invertebrates	**	0.14	*	0.08	*	0.04	*	0.06	***	**0.12**
Sediment matrix/ sessile invertebrates	***	**0.38**	**	0.06		0.01		0.01	***	0.15
Foliose red algae		0.02		0.03	**	0.04	**	0.03	**	**0.14**
Small boulders		0		2e-3		2e-3		0.02		**0.02**

Table 4. Results of 90th quantile regression analysis testing the relationship between the benthic habitat characteristics and the densities of *H. rubra* at different quadrat sizes 0.25x0.25 m, 0.5x0.5 m, 1x1 m, 2x2 m and 4x4 m, Maria Island. Values given are, p-values (p), and the coefficient of determination (R^{-1}). p≤0.05 are indicated by *, p≤5e-3 ** and p≤5e-4 ***. The largest values of R^{-1} for each habitat characteristics are indicated in bold-print.

Quadrat size	0.25x0.25 m		0.5x0.5 m		1x1 m		2x2 m		4x4 m	
Variables	**p**	R	**p**	R	**p**	R	**p**	R	**p**	R
NERA	*	0.02	**	0.06	*	**0.09**	*	**0.08**	**	0.05
NCA		0.01		0.01		0.01		9e-5		**0.02**
ERA	**	**0.16**	***	0.05	**	0.01		0.01	**	0.11
Sediment matrix	*	0.07	***	0.01	***	**0.08**		0		2e-3
Sessile invertebrates	***	0.02	***	0.02		0		0.01	**	**0.02**
Sediment matrix/ sessile invertebrates	***	0.42	***	**0.1**	***	0.04		0.01		0.01
Foliose red algae	**	**0.01**	**	**0.01**		0		1e-3		0.01
Overstorey brown algae		**0.01**		1e-3		0.01		0		0.01

At both locations, the relationship between the cover of sediment matrix and adult *H. rubra* densities was clearest at the smaller quadrat sizes (0.25x0.25 m, 0.5x0.5 m and 1x1 m), while the relationship between the cover of NERA and ERA and the densities of adult *H. rubra* was clearest at the smaller (0.25x0.25 m, 0.5x0.5 m, and 1x1 m) and the largest (4x4 m) quadrat sizes. Similarly, at George Third Rock, the relationship between the cover of NCA and the densities of adult *H, rubra* was clearest at the smaller (0.25x0.25 m, 0.5x0.5 m, 1x1 m) and largest (4x4 m) quadrat sizes. In contrast, at Maria Island there was no detectable relationship between the cover of NCA and the densities of adult abalone, irrespective of quadrat size.

At George Third Rock, the relationship between the cover of sessile invertebrates, and combined sediment matrix and sessile invertebrates, with density of adult *H. rubra* was clearest in the smallest (0.25x0.25 m) and largest (4x4 m) quadrat sizes. In contrast, at Maria Island, the cover of the sediment matrix, and of the matrix and sessile invertebrates combined with densities of adult *H. rubra* were most clearly evident at smaller scales (0.25x0.25m, 0.5x0.5 m and 1x1 m). The relationship between the cover of foliose red algae and the densities of adult *H. rubra* showed the opposite trend between the two locations. At George Third Rock, the relationship between the cover of foliose red algae and densities of adult *H. rubra* was clearest at the largest scale (quadrat size 4x4 m), while at Maria Island this relationship was clearest in the smallest (0.25x0.25 m) and largest quadrat sizes (4x4 m).

The effect of depth and site on the relationship between the benthic habitat characteristics and *H. rubra*

We used quantile regression to test whether, in the optimal quadrat sizes, the relationships between the common habitat characteristics with densities of adult *H. rubra* at each location, varied with depth and site. The analyses revealed that the relationship between the biotic factors and adult *H. rubra* densities varied with depth and site depending on the nature of the particular habitat characteristics (Figure 2, 3, 4, 5, Table 5, 6).

At George Third Rock, there were no detectable effects of depth or site on the negative association between extent of the cover of the sediment matrix and sessile invertebrates combined, or foliose red algae, and adult abalone densities. In contrast, in the smaller quadrat sizes (0.25x0.25 m and 0.5x0.5 m) there was a strong negative relationship between the cover of NCA and sessile invertebrates and the density of adult *H. rubra* at all sites, but not in shallow waters. Similarly, in the largest quadrat size (4x4 m), there was a strong negative relationship between the cover of the sediment matrix and adult abalone densities in deeper waters, but not in shallower waters, and no detectable effect of site. In the 0.25x0.25 m quadrat size, there was a strong positive relationship between the cover of NERA and adult abalone densities at both depths, and at the NE and SE sites, but not at the NW and SW sites, and in the 4x4m quadrat size there was a strong positive relationship between the cover of NERA and adult abalone densities at both depths, but not at any site. The positive relationship between the cover of NERA and the density of adult *H. rubra,* and the negative relationship between the cover of the sediment matrix, sessile invertebrates and adult abalone densities, in all of the other optimal quadrat sizes were consistent across depths and sites.

At Maria Island for the most part, relationships between benthic habitat characteristics did not vary with depth or across site. There were no detectable effects of depth on the positive relationship between NERA, ERA, and foliose red algae with densities of adult *H. rubra,* or on the negative relationship between the cover of the sediment matrix, sessile invertebrates, and the sediment matrix and sessile invertebrates combined and the densities of adult abalone. Similarly, there were also no detectable effects of site on the negative relationship between the cover of sessile invertebrates and adult *H. rubra* densities, or on the positive relationship between the cover of foliose red algae and the densities of adult abalone. Minor exceptions arose in the smallest (0.25x0.25 m) and largest (4x4 m) quadrat sizes, in which there was a consistent positive relationship between the cover of NERA and ERA and the densities of adult *H. rubra* at all sites, with the exception of Painted Cliffs. Similarly, in the 1x1 m quadrat size, was there a strong negative relationship between the extent of sediment matrix and densities of adult *H. rubra* at both depths and at all sites apart from Return Point. However, there was no detectable effect of site on the positive relationship between the cover of NERA, ERA and the densities of adult abalone, or on the negative relationship between the cover of the sediment matrix and adult *H. rubra* densities, in any of the other optimal quadrat sizes.

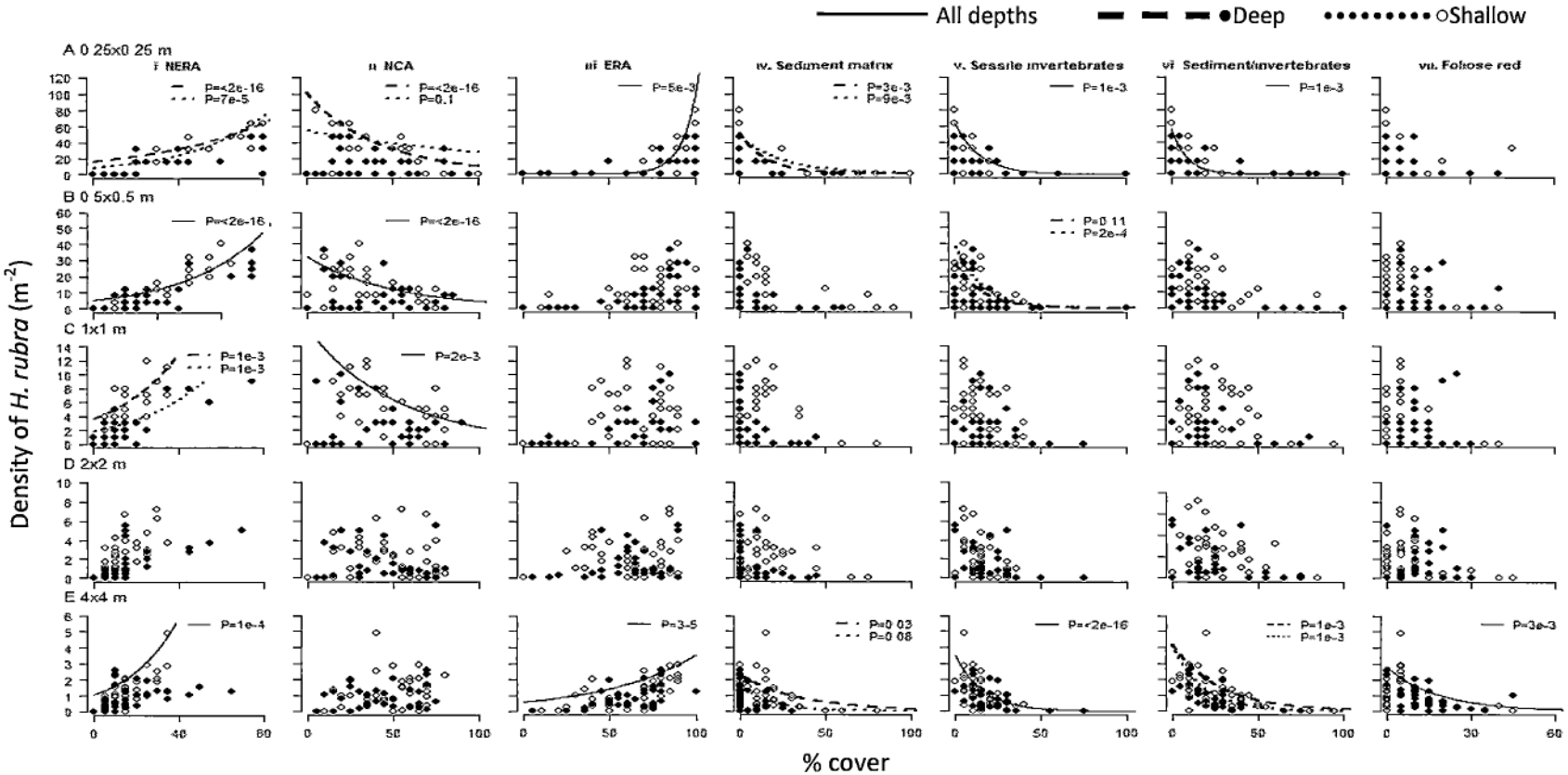

Figure 2. Effect of depth on the relationship between the density of *H. rubra* (m^{-2}) and the cover of (i) NERA, (ii) NCA, (iii) ERA, (iv) sessile invertebrates, (v) sediment matrix, (vi) sediment matrix and sessile invertebrates combined, and (vii) foliose red algae in quadrat sizes A. 0.25x0.25 m, B. 0.5x0.5 m, C. 1x1 m, D. 2x2 m and E. 4x4 m at George Third Rock. Results are the effects of depth and biotic factors, analysed using quantile regression models for the 90th quantile (see Table 8). Relationships (with p-values) are demonstrated for the optimal scales.

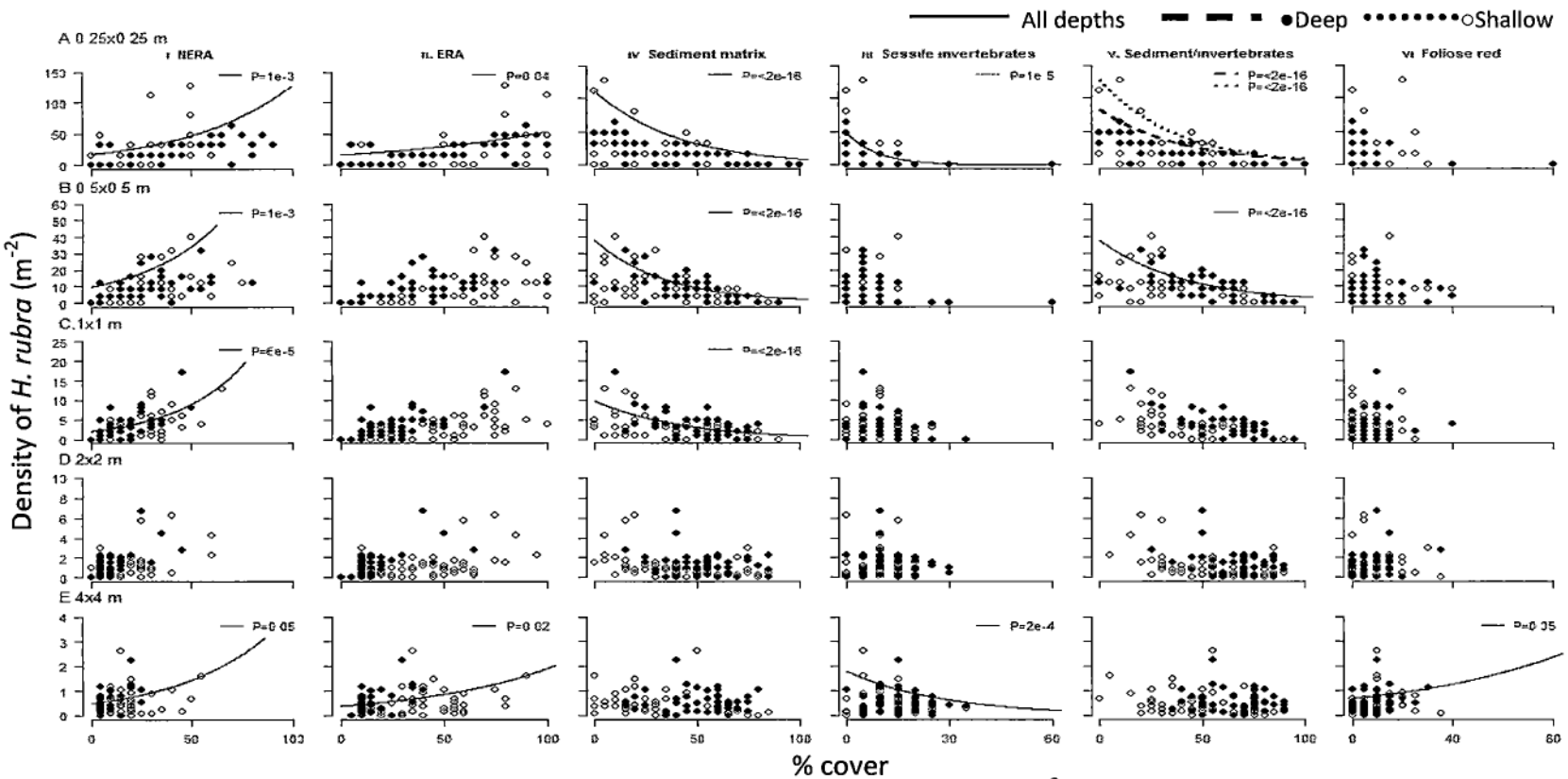

Figure 3. Effect of depth on the relationship between the density of *H. rubra* (m^2) and the cover of (i) NERA, (ii) ERA, (iii) sessile invertebrates, (iv) sediment matrix, (v) sediment matrix and sessile invertebrates combined, and (vi) foliose red algae in quadrat sizes A. 0.25x0.25 m, B. 0.5x0.5 m, C. 1x1 m, D. 2x2 m and E. 4x4 m at Maria Island. The effect of depth and the biotic factors, analysed using quantile regression models for the 90th quantile (see Table 9). Relationships (with p-values) are demonstrated for the optimal scales.

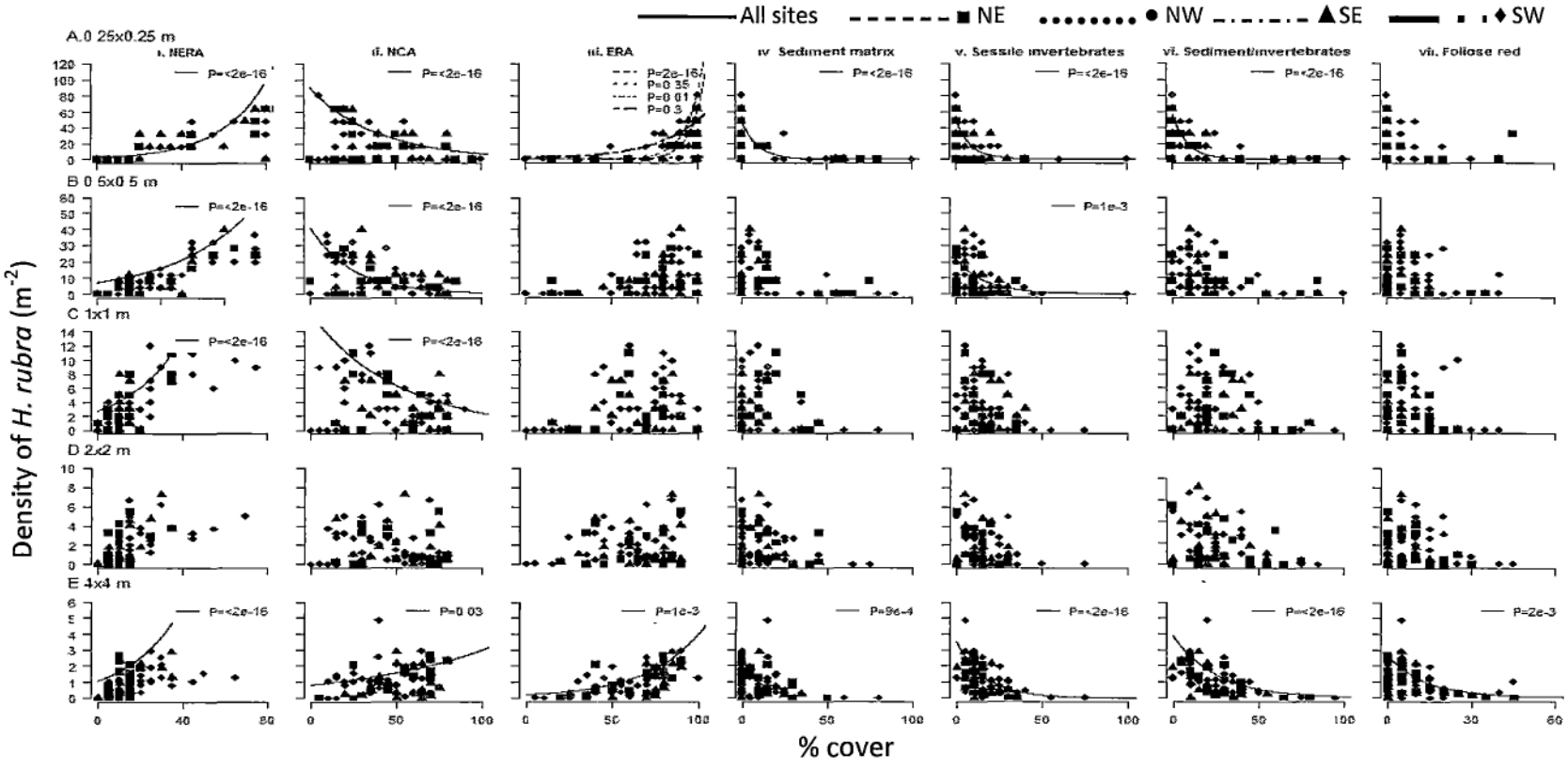

Figure 4. Effect of site on the relationship between the density of *H. rubra* (m^2) and the cover of (i) NERA, (ii) NCA, (iii) ERA, (iv) sessile invertebrates, (v) sediment matrix, (vi) sediment matrix and sessile invertebrates combined, and (vii) foliose red algae in quadrat sizes A. 0.25x0.25 m, B. 0.5x0.5 m, C. 1x1 m, D. 2x2 m and E. 4x4 m at George Third Rock. The effects of site and the biotic factors were analysed using quantile regression model for the 90^{th} quantile (see Table 10), 11). Relationships (with p-values) are demonstrated for the optimal scales.

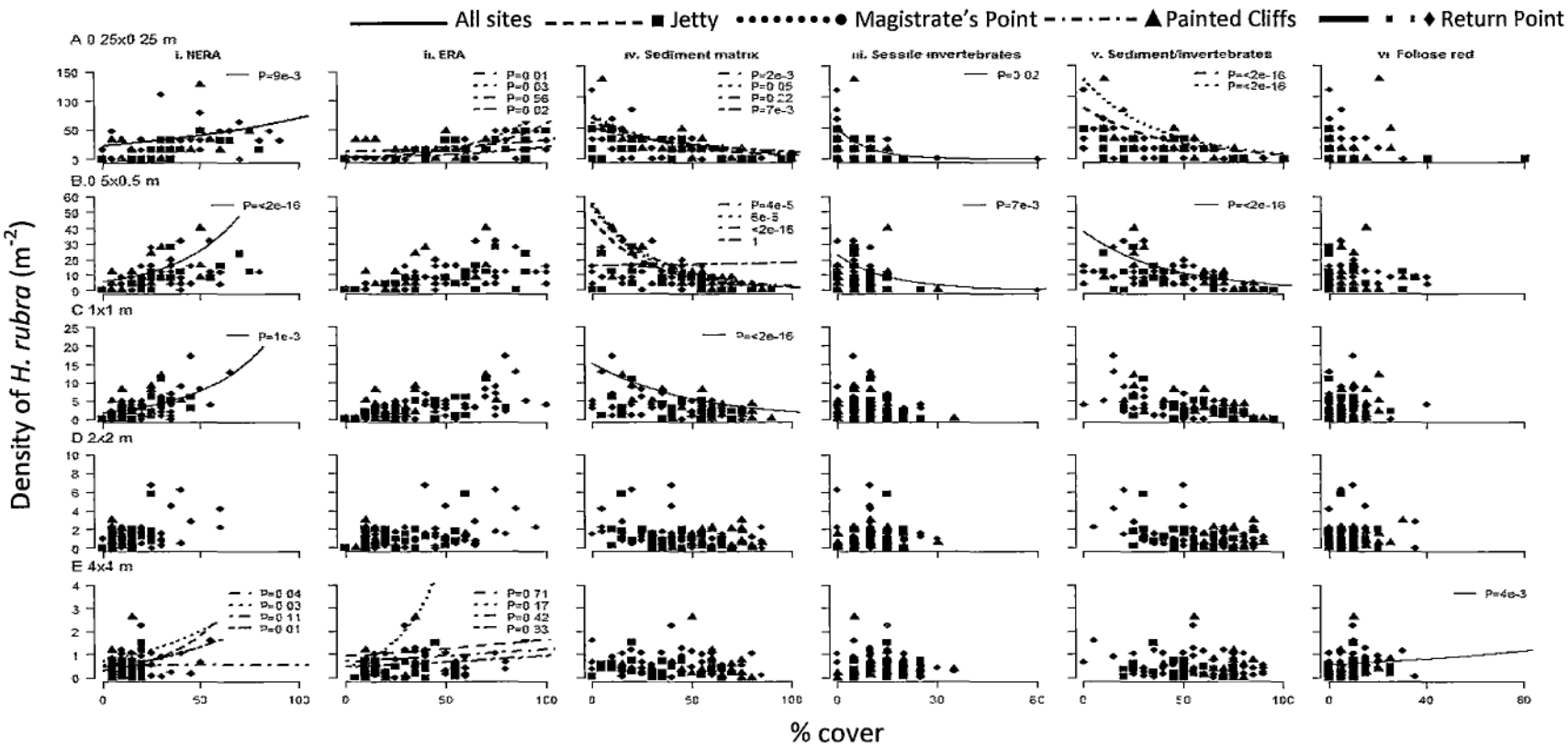

Figure 5. Effect of site on the relationship between the density of *H. rubra* (m^2) and the cover of (i) NERA, (ii) ERA, sessile invertebrates, (iii) sediment matrix, (iv) sediment matrix and sessile invertebrates combined, and (v) foliose red algae in quadrat sizes A. 0.25x0.25 m, B. 0.5x0.5 m, C. 1x1 m, D. 2x2 m and E. 4x4 m at Maria Island. The effects of site and the biotic factors were analysed using quantile regression models for the 90th quantile (see Table 12, 13). Relationships (with p-values) are demonstrated for the optimal scales.

Table 5. Results of quantile regression analysis of the 90th quantile relationship between the benthic habitat characteristics and the densities of *H. rubra,* at different depths on in the optimal quadrat sizes ranging between 0.25x0.25, 0.5x0.5, 1x1, 2x2, and 4x4 m, at George Third Rock. All data is pooled across sites and non-significant interactions are not reported. Values given are t-values and p-values. Significant p are indicated in bold-print.

Quadrat sizes	0.25x0.25 m	0.5x0.5 m	1x1m	2x2 m	4x4 m
NERA	8.68	9.32	3.79		3.34
	<2e^{-16}	**<2e^{-16}**	**2e^{-4}**		**1e^{-4}**
Depth	-2.26	-1.53	-2.73		-0.53
	0.03	0.13	**7e^{-3}**		0.6
NCA	-5.44	-6.21	-3.88		-1.9
	1e^{-4}	**<2e^{-16}**	**2e^{-3}**		0.06
Depth	-2.14	-1.73	-1.72		-1.45
	0.04	0.09	0.08		0.15
ERA	2.87				4.38
	5e^{-3}				**3e^{-5}**
Depth	-0.23				-1.25
	0.83				0.22
Sediment matrix	-2.25				-6.42
	0.03				**<2e^{-16}**
Depth	-0.41				-4.42
	0.69				**3e^{-5}**
Sediment matrixxDepth	-2.52				
	0.02				
Sessile invertebrates	-4.03	-6.65			-11.84
	1e^{-4}	**<2e^{-16}**			**<2e^{-16}**
Depth	-1.15	-7.74			-0.02
	0.26	**<2e^{-16}**			0.1
Sediment matrix/ invertebrates	-3.4				-9.51
	1e^{-3}				**1e^{-4}**
Depth	-0.24				-2.38
	0.82				**0.03**
Foliose red algae					-3.7
					3e^{-3}
Depth					-0.2
					0.37

Table 6. Results of quantile regression analysis of the 90th quantile relationship between the benthic habitat characteristics and the densities of *H. rubra,* at different depths, in the optimal quadrat sizes ranging between 0.25x0.25 m, 0.5x0.5 m, 1x1 m, 2x2 m and 4x4 m, at Maria Island. All data is pooled across sites and non-significant interactions are not reported. Values given are t-values and p-values. Significant p are indicated in bold print.

Quadrat sizes	0.25x0.25 m	0.5x0.5m	1x1 m	2x2 m	4x4 m
NERA	4.4	3.22	4.21		1.95
	1e^{-3}	**1e-3**	**6e^{-5}**		**0.05**
Depth	-1.84	-0.5	1.34		1.3
	0.07	0.62	0.19		0.2
ERA	3.89				2.42
	0.04				**0.02**
Depth	-0.58				1.6
	0.57				0.12
Sediment matrix	-7.44	-7.04	-6.79		
	<2e^{-16}	**<2e^{-16}**	**<2e^{-16}**		
Depth	-1.78	-0.02	-1.96		
	0.08	0.9	0.06		
Sessile invertebrates	-5.59	-1.07		-1.93	-3.83
	1e^{-5}	0.29		0.06	**2e^{-4}**
Depth	-1.68	0.52		-0.27	0
	0.1	0.61		0.8	1
Sediment matrix/	-10.78	-8.67			
invertebrates	**<2e^{-16}**	**<2e^{-16}**			
Depth	-2.9	1.4			
	3e^{-4}	0.17			
Foliose red algae	0	-1.1			2.01
	1	0.28			**0.05**
Depth	0	0.33			0.12
	1	0.74			0.91

Table 7. Results of quantile regression analysis of the 90th quantile relationship between the benthic habitat characteristics and the densities of *H. rubra,* at different sites, in the optimal quadrat sizes ranging between 0.25x0.25 m, 0.5x0.5 m, 1x1 m, 2x2 m and 4x4 m, at George Third Rock. All data is pooled across depth and non-significant interactions are not reported. Values given are t-values and p-values. Significant p are indicated in bold-print.

Quadrat sizes	0.25x0.25 m	0.5x0.5 m	1x1 m	2x2 m	4x4 m
NERA	6.79	14.97	5.67		5.45
	<2e^{-16}	**<2e^{-16}**	**<2e^{-16}**		**<2e^{-16}**
NW	1.14	1.01	-0.22		-1.25
	0.26	0.32	0.83		0.27
SE	1.94	1.04	-0.06		-0.95
	0.06	0.31	0.94		0.35
SW	0.24	-0.9	-0.92		-1.26
	0.8	0.37	0.36		0.21
NCA	-6.38	-7.32	-5.38		2.22
	<2e^{-16}	**<2e^{-16}**	**<2e^{-16}**		**0.03**
NW	0.16	0.94	-0.69		-0.28
	0.88	0.36	0.49		0.79
SE	1.16	1.05	-0.46		0.17
	0.25	0.3	0.65		0.87
SW	-0.12	0.79	0.1		1.26
	0.91	0.43	0.93		0.22
ERA	6.99				4.31
	<2e^{-16}				**1e^{-3}**
NW	1.61				1.19
	0.11				0.24
SE	3.93				-1.06
	1e^{-3}				0.29
SW	1.89				0.85
	0.06				0.4
Sediment matrix	-12.22				-2.64
	<2e^{-16}				**9e^{-4}**
NW	0.7				0
	0.49				1
SE	0.76				-0.38
	0.45				0.71
SW	0				0.46
	1				0.65
Sessile	-4.98	-3.63			-6.07

invertebrates	**$<2e^{-16}$**	**$1e^{-3}$**	**$<2e^{-16}$**
NW	1.08	1.43	1.93
	0.29	0.16	**0.06**
SE	0	0.41	-0.04
	1	0.68	0.7
SW	0.99	0.02	0.52
	0.33	0.97	0.61
Sediment matrix/	-17.5		-5.48
sessile invertebrates	**$<2e^{-16}$**		**$<2e^{-16}$**
NW	0.77		0.06
	0.45		0.96
SE	0.25		-1.14
	0.81		0.26
SW	1.32		0.31
	0.19		0.76
Foliose red algae			-3.84
			$2e^{-3}$
NW			0.89
			0.38
SE			0.12
			0.91
SW			1.87
			0.06

Table 7. Results of quantile regression analysis of the 90th quantile relationship between the benthic habitat characteristics and the densities of *H. rubra,* at different sites, in the optimal quadrat sizes ranging between 0.25x0.25 m, 0.5x0.5 m, 1x1 m, 2x2 m and 4x4 m, at Maria Island. All data is pooled across depth and non-significant interactions are not reported. Values given are t-values and p-values. Significant p are indicated in bold-print.

Quadrat sizes	0.25x0.25 m	0.5x0.5 m	1x1 m	2x2 m	4x4 m
NERA	2.67	5.01	4.46		4.33
	$9e^{-3}$	**$<2e^{-16}$**	**$1e^{-3}$**		**$4e^{-5}$**
Magistrate's Point	0.07	0	0.52		2.88
	0.95	1	0.61		**$5e^{-3}$**
Painted Cliffs	0.71	1.49	1.65		1.37
	0.48	0.14	0.11		0.17
Return Point	1.23	0.88	0.84		0.4
	0.23	0.38	0.41		0.7
ERA	3.99				2.25
	$2e^{-3}$				**0.03**
Magistrate's Point	1.47				2.78
	0.15				**$7e^{-3}$**
Painted Cliffs	2.48				1.32
	0.02				**$7e^{-3}$**
Return Point	0.55				0.40
	0.59				0.69
Sediment matrix	-14.93	-13.94	5.48		
	$<2e^{-16}$	**$<2e^{-16}$**	**$2e^{-16}$**		
Magistrate's Point	-1.19	1.27	0.17		
	0.24	0.21	0.87		
Painted Cliffs	2.18	3.11	0.92		
	0.03	**$2e^{-3}$**	0.36		
Return Point	1.5	3.1	0.7		
	0.14	**2e-3**	0.49		
Sessile invertebrates	-2.38	-2.77		-0.03	-0.6
	0.02	**$7e^{-3}$**		0.31	0.55
Magistrate's Point	-1.02	-0.78		0.07	0.37
	0.314	0.44		0.93	0.71
Painted Cliffs	-1.84	0		-0.13	0.41
	0.06	1		0.82	0.69
Return Point	0	0.73		-0.14	0.46
	1	0.47		0.82	0.65
Sediment matrix/ invertebrates	-5.96	-16,15			
	$<2e^{-16}$	**$<2^{e-16}$**			

Magistrate's Point	0.48	0	
	0.64	1	
Painted Cliffs	0.68	1.52	
	0.5	0.13	
Return Point	0.36	3.78	
	0.72	**$2e^{-4}$**	
Foliose red algae	0	-0.02	3.03
	1	0.13	**$4e^{-3}$**
Magistrate's Point	-1.28	-0.55	1.02
	0.21	0.59	0.32
Painted Cliffs	0	0.42	0.32
	1	0.68	0.76
Return Point	0	0.17	1.05
	1	0.87	0.3

DISCUSSION

Our study has described quantitatively the effect of benthic habitat characteristics, as single variables and guilds, on the density adult *Haliotis rubra* in an exposed and sheltered location, across two depths and several sites within each location. We also identified the spatial scale(s) at which these relationships were most clearly defined. Our results revealed no detectable relationship between any of the habitat characteristics and the average shell length of adult *H. rubra*. There were also no clear relationships between the abiotic habitat characteristics and density of adult *H. rubra*. In contrast, several of the biotic factors were important in explaining the densities of adult *H. rubra* and the strength of the relationship between biotic features and densities of adult abalone varied with the scale of observation. We argue that identifying the scales at which patterns are most clearly in focus allows us to suggest, and subsequently test, possible underlying casual mechanisms governing the way in which habitat features influence *H. rubra*, and how abalone influence habitat features.

Associations between biotic habitat characteristics and *H. rubra*

At both locations, the biotic habitat characteristics most important in explaining the densities of adult *H. rubra* included the cover of non-calcareous encrusting red algae (NERA), non-geniculate coralline algae (NCA), encrusting red algae (ERA, combined NERA and NCA), the sediment matrix that develops with small filamentous algae, sessile invertebrates, and foliose red algae. The direction and strength of the

relationship between these biotic factors or guilds and densities of adult *H. rubra* differed between quadrat sizes.

Overall, abalone density was positively associated with cover of NERA and ERA, but declined with increasing cover of the sediment matrix, sessile invertebrates, and the combined cover of sediment matrix and sessile invertebrates, at small spatial scales (0.625 m^2, 0.25 m^2, and 1 m^2). These results are consistent with other observations on the east coast of Tasmania and worldwide (Shepherd 1973, Nash et al. 1995, Kitting 1997, Daume et al. 1999, Miner et al. 2007, Valentine et al. 2008). The nature and direction of these relationships requires further investigation. At present, it is not clear whether adult abalone are simply associated with habitat dominated by NERA and ERA or whether they are also important in maintaining it.

One possible explanation of the nature of these relationships at very local is linked to adult abalone behaviour. NERA and ERA are thin, tightly adherent crusts and their relatively smooth surfaces are highly suitable for adherence of adult *H. rubra,* helping to prevent dislodgement in turbulence (Steneck 1982), facilitating protection from predators (Shepherd & Turner 1985), and/or allowing increased access to food (Steneck 1982). In contrast, the relatively loose and semi-consolidated sediment matrix, and sessile invertebrates, are likely prevent or limit abalone attachment, potentially increasing physical stresses and losses to predator (Shepherd & Turner 1985). Thus, it should be examined whether adult abalone could actively seek habitat covered by NERA and ERA and avoid areas covered by sediment and sessile invertebrates.

Herbivores are one of the most important disturbances that enable the prevalence of ERA (Steneck 1986). It is also possible that adult *H. rubra* is not only attracted to habitat dominated by NERA and ERA but that it might be also directly involved in maintaining algal crust dominated by NERA and ERA, at local scales, by keeping the crusts free from overgrowth by filamentous and foliose algae and sessile invertebrates, and smothering by the sediment matrix.. If adult abalone activity is important in maintaining this habitat type, both bulldozing (Dayton 1971, Hawkins 1983) and direct grazing (Leighton & Boolootian 1963, Shepherd, 1973) may be involved. Further study is required to understand whether adult *H. rubra* play an important role in maintaining patches of NERA and ERA on rocky reefs.

Scale dependent relationships between the biotic habitat characteristics and *H. rubra*

The patterns reported here provide a starting point for further investigations on the effects of biotic habitat characteristics on the distribution and densities of adult *H. rubra.* Our results demonstrate that, in general, relationships between many of the biotic habitat factors are clearest at the smaller spatial scales (0.0625 m^2, 0.25 m^2, and 1 m^2). This suggests that adult *H. rubra* could respond to and/or influence features of the benthic rocky reef at these spatial scales. Our results are consistent with other research which has demonstrated that many adult abalone typically move only small distances per day (>30 mm) although some individuals can moved much further (Landsdell 2006, Prince 1989, Chapter 2).

There were also a limited number of biotic habitat characteristics that were important in explaining the densities of adult *H. rubra* at the largest spatial scale we considered (16 m^2). At both locations, there was a weak positive relationship between the cover of NERA and ERA and the densities of adult *H. rubra* in the largest quadrat size. Similarly, broad scale surveys on the east coast of Tasmania demonstrated a weak but none-the-less significant positive relationship between the cover of ERA and the densities of *H. rubra* in 25x25 m quadrats (Valentine et al. 2008). These results suggest that the positive relationship between the cover of NERA, and ERA, with the densities of adult *H. rubra* is scalable. The relationship will break down at sites where other mechanisms are more important for maintaining ERA largely free of overgrowth by filamentous and foliose algae and sessile invertebrates e.g. low light and canopy sweep (Connell 2003).

Effect of location, depth, and site on relationships between habitat characteristics and *H. rubra*

We tested the way in which relationships between biotic habitat characteristics and the densities of adult *H. rubra* vary with depth and across sites within the two locations and found no consistent effects. The only significant effects were evident at the smaller (0.25x0.25 m and 0.5x0.5 m) and largest (4x4 m) quadrat sizes, where some relationships significantly varied with depth at George Third Rock and with site at Maria Island. For example, at George Third Rock, in the smaller quadrat sizes, there was a significant negative relationship between the cover NCA and sessile invertebrates and the density of adult *H. rubra* in deep but not in shallow waters. These results could be explained by the differences in exposure between shallow and depth waters at George Third Rock. At Maria Island, in

the smallest and largest quadrat sizes there was a positive relationship between the cover of ERA and the densities of adult *H. rubra,* a negative relationship between the cover sessile invertebrates and adult abalone density, at all sites except at Painted Cliffs. However, abalone were relatively rare at Painted Cliffs, which could explain these differences. Irrespective, the major differences in the effect of the biotic habitat characteristics on densities of adult *H. rubra* were between the two locations.

Differences in the patterns between the two locations suggest new insights. At George Third Rock, in the smaller quadrat sizes (0.25x0.25 m and 0.5x0.5 m), there was a negative relationship between the cover of NCA and the densities of adult *H. rubra* and in the largest quadrat size (4x4 m) there was a negative relationship between the cover of foliose red algae and adult abalone densities. In contrast, at Maria Island in the smaller quadrat sizes (0.25x0.25 m and 0.5x0.5 m), there was no detectable relationship between the cover of NCA and the densities of adult *H. rubra* and in the largest quadrat size (4x4 m) there was a positive relationship between the cover of foliose red algae and abalone densities. These differences may reflect dissimilar variances in the relationships between the habitat features and densities of *H. rubra* (0.25x0.25 m GIII variance=480.21, MI variance=439.89, 0.5x0.5 m GIII variance=99.7, MI variance=66.7 and 4x4 m GIII variance=0.77 and MI variance=0.21), differences in the algal abundances and species composition, wave exposure, or habitat complexity, between the two locations. Alternatively there could be differences in responses of abalone to the different algal species at the two locations, or a non-linear behavioural response to different absolute amounts of these species in these functional groups (NCA, and foliose red algae) (Shepherd 1973, Shepherd & Steinberg 1992). However, since we only examined two locations, one exposed and one sheltered, it was not possible to test these ideas.

Methods for testing the relationship between habitat characteristics and *H. rubra*

Because any one approach is likely to have limitations, we used three methods (BEST, Generalized Linear Modelling and quantile regression) to examine the relationships between biotic habitat characteristics on the densities of adult abalone. For each quadrat size, we used BEST and GLM to identify the habitat characteristics that were most highly correlated or that explained a large percentage of the variation in the densities of adult *H. rubra* across depth and sites. Our results demonstrate that the relationships

between the individual and combined habitat characteristics and the densities of adult *H. rubra* identified by BEST and GLMs were, in general, weak. However, Cohen (1998) has suggested that even low correlation values can still signify important weak effects and Hall (1990) suggested that variance percentages as low as 10% can be ecologically meaningful. The limitations of the BEST and GLM analyses reflect the distribution of the data, which described as factor-ceiling relationships.

To address these limitations, we used quantile regression to estimate the limiting effects of six important biotic predictors on densities of *H. rubra,* at several spatial scales. We found that there were negative and positive relationships between the six biotic habitat characteristics and the densities of adult *H. rubra,* and that these relationships were in general, clearest at smaller spatial scales. Our results could be used to predict areas at small-scales where the habitat might be suitable to increase densities of adult *H. rubra.* However, the quantile regression does not, of course take into account other features of the available habitat that we did not measure such as resource availability, intraspecific and interspecific competition, or predation and the effects of fishing (Vaz et al. 2008). Overall, we found that the three approaches were complementary however, quantile regression had several advantages over BEST and GLM for quantifying the relationships between the biotic habitat characteristics and densities of adult *H. rubra* given its capability to deal with a wide range of data distributions and zero-inflated data (Cade et al. 1999).

It is important not to infer too much about the processes that may underpin the patterns we observed. What we have presented is a 'snapshot' of the association between habitat characteristics and adult *H. rubra* in time and space. Not all potential habitat characteristics were included in the analyses. We did not consider temporal variation in the patterns observed. Despite these limitations, our results demonstrated that there are important relationships between biotic habitat characteristics and densities of adult *H. rubra,* that are particularly meaningful at small spatial scales and for a limited number of biotic habitat characteristics at the largest spatial scales. Experimental manipulations of habitat availability and *H. rubra* densities are necessary to confirm the causal mechanisms behind these observed relationships.

Our results could have important implications for *H. rubra* fisheries dynamics depending on the underlying processes involved. If adult *H. rubra*

activities are responsible for maintaining ERA free from the sediment matrix, filamentous and foliose algae and sessile invertebrates then intensive fishing of individual abalone is likely to result in small-scale changes to the benthic community, and collectively at larger scales. Alternatively, if adult *H. rubra* are responding to particular biotic habitat characteristics then intensive fishing of abalone is unlikely to have a major impact on the benthic habitat. Understanding the potential dynamic interplay between the effect of the biotic habitat features on adult *H. rubra* and/or the effects of adult abalone on biogenic habitat characteristics is clearly important for abalone fisheries management.

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Appendix 1. Results of BEST analyses yielding the best rank order matches between similarity matrices based on benthic habitat characteristics and equivalent matrices based on densities of *H. rubra* at George Third Rock for the top ten variables in the 0.25x0.25 m, 0.5x0.5, 1x1 m, 2x2 m and 4x4 m quadrat sizes. The values given for each individual or group of variables are the Spearman's rank correlation coefficient (Rho).

Quadrat size				
0.25x0.25 m	**0.5x0.5 m**	**1x1 m**	**2x2 m**	**4x4 m**
Small boulders 0.2	NERA 0.6	NERA 0.33	NERA 0.29	ERA 0.38
E. radiata 0.11	ERA 0.32	ERA 0.32	ERA 0.23	NERA 0.38
ERA 0.08	Small boulders 0.16	NCA 0.21	NCA 0.21	NCA 0.28
ERA 0.06	Sediment matrix/ sessile invertebrates 0.14	Sediment matrix/ sessile invertebrates 0.17	*C. confluens* 0.17	*E. radiata* 0.23
Branching coralline 0.05	NCA 0.13	*E. radiata* 0.15	Foliose red algae 0.17	Small boulders 0.23
Foliose red algae 0.05	Foliose red algae 0.08	Sessile invertebrates 0.13	Understorey foliose brown algae 0.16	*Zonaria* spp. 0.16
C. confluens 0.05	Bare rock 0.07	Small boulders 0.13	Small boulders 0.14	Understorey foliose brown algae 0.15
NCA 0.01	Branching coralline 0.07	Foliose red algae 0.13	Sessile invertebrates 0.12	Foliose red algae 0.15
Sediment matrix/ sessile invertebrates 0.01	*P. comosa* 0.03	*C. remotifolia* 0.12	Sediment matrix/ sessile invertebrates 0.09	Sessile invertebrates

Sessile invertebrates 0.01	Sessile invertebrates 0.02	*C. confluens* 0.1	Foliose red algae 0.04	0.13 *D. potatorum* 0.12

Appendix 2. Results of BEST analyses yielding the best rank order matches between similarity matrices based on benthic habitat characteristics and equivalent matrices based on densities of *H. rubra* at Maria Island for the top ten variables in the 0.25x0.25 m, 0.5x0.5, 1x1 m, 2x2 m and 4x4 m quadrat sizes. The values given for each individual or group of variables are the Spearman's rank correlation coefficient (Rho).

Quadrat size				
0.25x0.25 m	**0.5x0.5 m**	**1x1 m**	**2x2 m**	**4x4 m**
NERA 0.37	NERA 0.51	NERA 0.34	*Sargassum* spp. 0.15	Other foliose green algae 0.19
ERA 0.37	ERA 0.43	ERA 0.28	Understorey foliose brown algae 0.13	Sessile invertebrates 0.11
Sediment matrix/ sessile invertebrates 0.21	NCA 0.25	NCA 0.19	NCA 0.11	*Zonaria* spp. 0.1
Sediment matrix 0.15	Overstorey brown algae 0.13	Overstorey brown algae 0.18	ERA 0.11	Other understorey foliose brown algae 0.07
NCA 0.14	*Sargassum* spp. 0.11	*Sargassum* spp. 0.12	NERA 0.11	NCA 0.07
Sargassum spp. 0.08	Sediment matrix/ sessile invertebrates 0.1	*Zonaria* spp. 0.1	Sessile invertebrates 0.09	ERA 0.06
Overstorey brown algae 0.06	Sediment matrix 0.07	Other foliose green algae 0.07	*Zonaria* sp. 0.08	Flat rock 0.05
Bare rock 0.04	Understorey foliose brown algae 0.05	Large boulders 0.07	Other foliose green algae 0.07	*Sargassum* spp. 0.05

C. flexis 0.04	Other foliose green algae 0.05	Sediment matrix/sessile invertebrates 0.04	*P. comosa* 0.05	Filamentous red algae 0.05
P. comsa 0.03	*Cystophera* spp. 0.05	Foliose green 0.03	Large boulders 0.04	NERA 0.05

CHAPTER 6: INTENSIVE FISHING OF ABALONE CAUSES A SHIFT TO BENTHIC HABITAT TYPES POORLY PREFERRED BY ABALONE.

ABSTRACT

Fishing is a widespread and exploitative activity, that can cause dramatic shifts in species composition, which are often long lasting and difficult to reverse. We used 3 approaches to tested whether intensive fishing of blacklip abalone (*Haliotis rubra*) leads to a shift in benthic habitat and which subsequently affects the distribution and abundance of adult abalone, at 2 locations, and 4 sites, on the east coast of Tasmania, Australia. After 18 months of removing abalone from rocks, non-calcareous encrusting red algae (NERA) and non-geniculate coralline algae (NCA), became overgrown by filamentous and foliose algae, sessile invertebrates, and accumulation of sediment. The differences in detailed community composition between locations were minor. These results suggest *H. rubra* grazing is important in structuring Tasmania's subtidal rocky reef communities. Throughout our study *H. rubra* had a disproportionately high association with areas of rock covered in NERA and NCA, but avoided other habitat types. A transplant experiment demonstrated that adult *H. rubra* preferred areas of rock covered in NERA and NCA but actively move away areas overgrown by filamentous and foliose algae, sessile invertebrates, and accumulated sediment matrix. Our results suggest the relationship between *H. rubra* NERA and NCA mutualisitc and that intensive fishing of abalone may cause a shift to an alternative benthic habitat that is unfavourable for abalone. This establishes a positive feedback loop which is likely to establish the new habitat as an alternative and stable configuration of the benthos.

Keywords: Fishing, Regime shift, Alternative states, *Haliotis rubra*

INTRODUCTION

Fishing of marine consumers can cause caused dramatic shifts between alternative stable states, known as catastrophic, phase or regime shifts (Scheffer et al. 2001, Hughes et al. 2005). Examples of fisheries driven regimes shifts with severe economic and social consequences include, overgrowth of coral reefs by algae (Knowlton 1992, Mumby et al. 2007), transitions between kelp forests and turfing algae (Steneck 2002), formation of urchin barrens (Chapman & Johnson 1990, Tegner & Dayton 2000), and the irreversible collapse of many coastal and oceanic fish-stocks (Jackson et al. 2001, Meyers & Worm 2003, Ward & Myers 2005). These alternative states can persist indefinitely and are maintained by internal reinforcing processes and stabilized by negative feedback loops (Scheffer et al. 2001, Beisner et al. 2003, Collie et al. 2004). Although many studies have implicated fishing as a primary driver in marine regime shifts, relatively few have investigated the dynamics of the transition or the processes that maintain the stability of the new state, particularly for spatially complex systems (Scheffer & Carpenter 2003, Schroder et al. 2005).

Regime shifts can occur over a range of temporal and spatial scales, and not all organisms in the ecosystem are necessarily involved in, or influenced by the shift (Scheffer & Carpenter 2003, Hughes et al. 2005). Examples have been documented on spatial and temporal scales ranging from a few meters or years (Petritis & Latham 1999, Konar & Estes 2003) to basin scales of thousands of kilometers or decades (Jackson et al. 2001, Ward & Myers 2005). This temporal and spatial variability can make regime shifts and their consequences difficult to predict (Scheffer et al. 2001). Studies examining the effect of intensively harvesting marine consumers across a range of temporal and spatial scales are clearly required to better understand and manage the processes that result in regime shifts (Scheffer & Carpenter 2003, Hughes et al. 2005). Here we investigated whether intensive fishing of blacklip abalone (*Haliotis rubra*) can lead to changes in benthic habitat structure, and whether these changes subsequently affect the distribution and abundance of abalone on subtidal rocky reef ecosystems on the east coast of Tasmania, Australia.

Effects of fishing *H. rubra* on benthic habitat

Haliotis rubra is a large and abundant macro-invertebrate, found across a wide range of habitats and wave exposures in southeast Australia (Shepherd 1973). This species forms the basis of the world's largest abalone wild fishery and is subject to intense fishing pressures (Jenkins 2004). *H. rubra* activities may be important in structuring the benthos of rocky reefs on the east coast of Tasmania, Australia. Anecdotal evidence from abalone fishers and researchers alike suggests that intensive fishing of *H. rubra* populations leads to overgrowth of non-calcareous encrusting red algae (NERA) and non-geniculate coralline algae (NCA) by filamentous and foliose algae and sessile invertebrates, and accumulation of sediment. These observations suggest the possibility of cause and effect, but the idea requires critical testing. If *H. rubra* plays a key role in maintaining areas dominated by NERA and NCA then substantial reductions in their biomass and abundance through fishing could lead to a shift in the structure of understorey assemblages.

Effect of regime shift on *H. rubra* populations

Intensive fishing of *H. rubra* is likely to disrupt feedbacks in interaction topologies that involve abalone, and can be particularly important in the case of positive feedbacks, given their potential to be stabilizing with respect to one particular dynamic or community configuration but destabilizing to another (Beisner et al. 2003, Scheffer & Carpenter 2003). NERA and NCA provide metamorphogenic cues for *H. rubra* larvae (Daume et al. 1999), and their epiphytic microflora, as well as the algae themselves, are an important component of the diet of juvenile *H. rubra* (Shepherd & Turner 1985). Shell pigmentation associated with this feeding activity aids in camouflage, and so arguably provides indirect protection for juvenile *H. rubra* (Shepherd & Turner 1985). There is also a strong positive association between adult *H. rubra* and homescars covered by NERA and NCA (Chapter 5). Thus, the interaction between *H. rubra* and NERA and NCA could be characterised as a positive feedback loop; NERA and NCA promote settlement, growth and survivorship of abalone while abalone grazing promotes NERA and NCA. If intensive fishing of *H. rubra* disrupts this relationship and the benthos changes, there may be important implications for the long-term persistence of abalone populations.

Research questions

We used a series of experimental manipulations to examine the ecosystems effect of fishing *H. rubra* on subtidal rocky reef communities on the east coast of Tasmania, Australia. The 3 main questions were: (1) does heavy depletion of *H. rubra* lead to overgrowth of NERA and NCA with concomitant accumulation of sediment? (2) at what spatial and temporal scale are any changes in benthic habitat evident? and (3) does overgrowth of NERA and NCA have any effect on the behaviour and local abundances of adult *H. rubra*?

MATERIALS AND METHODS

Site characteristics

Manipulative experiments were conducted at four sites, located within two no-take marine reserves on the east coast of Tasmania, between spring 2004 and summer 2007 (Figure 1). Two sites were in an exposed location (George Third Rock research area) and two in a sheltered location (Maria Island marine reserve). At both locations, fishing of *Haliotis rubra* is prohibited and there are large numbers of abalone relative to surrounding fished areas (Prince 1989, Edgar & Barrett 1999). All manipulations took place on the deep edge of the reef where previous research showed that there are locally high densities of *H. rubra* (Chapter 5).

The sites at Maria Island were characterized by gently sloping rocky substratum to a depth of 9 m with moderate topographic relief. These randomly selected sites were located near the Jetty at Darlington Harbor and at Magistrate's Point. Both are sheltered from all but south-westerly swells, and support a diverse algae assemblage (Edgar 1984). The two sites are dominated by the overstorey species, *Cystophora retroflexa* and *Sargassum fallax.* The understorey community consisted of *Caulpera flexilis,* foliose and filamentous algae (largely red), non-calcareous encrusting red algae (NERA), non-geniculate coralline algae (NCA) and sessile invertebrates, with low levels of a matrix of filamentous algae and accumulated sediment on some rocks.

The two randomly selected sites at George Third Rock were characterized by gently sloping rocky substratum to a depth of 19 m with moderate topographic relief, and were located on the southwest and southeast margins of the reef. Both sites are similarly exposed to south-easterly swells and

classified as moderately exposed with a diverse algal assemblage (Edgar 1984). The principal overstorey species at the sites included *Ecklonia radiata, Phyllospora comsa,* and *Xiphophora gladiata* (Prince 1987). The understorey community included a variety of foliose red algae, NERA, NCA, and sessile invertebrates.

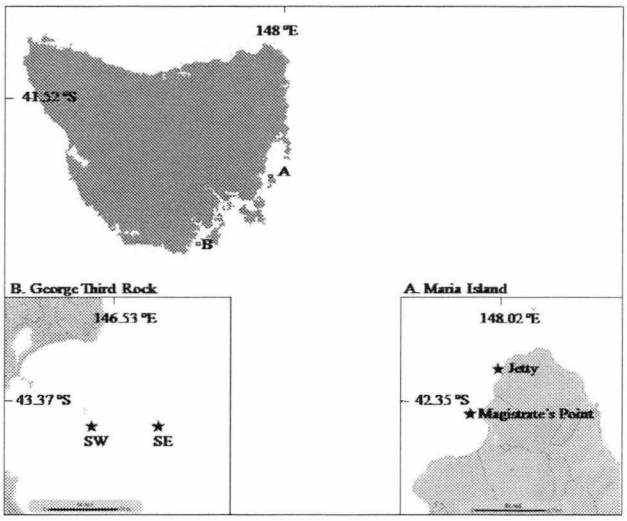

Figure 1. Map of the east coast of Tasmania, Australia, showing the locations, George Third Rock and Maria Island and the 4 study sites within each region.

Experimental manipulations

At Maria Island, we randomly selected ten individual rocks or groups of rocks (~2x1x0.5 m) supporting ≥3 *H. rubra,* at both sites On each rock 3 homescars (an area of continuous NERA and NCA directly under the abalone) and 3 randomly selected other positions in abalone habitat were selected and marked as fixed 0.15x0.15 m quadrats. Leader sheep ear tags (12x2 mm) were attached with epoxy resin (Z-spar A-788) to mark the corners of each fixed quadrat. Rocks were assigned randomly to treatments of either 0 or 100% removals of *H. rubra* (n=5 replicates of each) at each site.

At George Third Rock, a pilot study showed that monthly removals of *H. rubra* from rocks were insufficient to maintain experimental conditions

because, unlike at Maria Island abalone would rapidly recolonise rocks from which they were removed. Therefore we used a different experimental design at this location. Twelve individual rocks or groups of rocks (~2x2x1 m) supporting ≥3 *H. rubra* at both sites were selected randomly and 3 homescars and 3 other positions on each rock marked as outlined above. Four experimental treatments were allocated randomly (n=3 replicates of each treatment at each site):

Treatment 1:100% removal of *H. rubra,* no fences

Treatment 2:0% removal of *H. rubra,* no fences

Treatment 3:100% removal of *H. rubra,* fenced rocks

Treatment 4:0% removal of *H. rubra,* partially fenced rocks

Complete and partial fences were set up ~1 m away from the rocks. All fences were made of nylon monofilament netting (1.5 m radius, 0.5 m height and mesh size 50 mm). Two rows of chain lined the bottom of the mesh, which was secured to the bottom using star pickets. None of the fences had roofs while partial fences surrounded 60% of the rock. Fences were checked monthly and cleaned of accumulated algae and sediment.

Number of *H. rubra*

At the beginning of the experiment the total number of *H. rubra* on all rocks were counted. Divers then removed all *H. rubra* (shell length ranging between 40-210 mm at Maria Island and 20-189 mm at George Third Rock) from the removal treatment rocks and from a 1 m buffer area surrounding the rocks. All treatments were maintained during monthly visits, and each month the total number of *H. rubra* on each rock was recorded.

Effects of removing *H. rubra* on benthic community structure

On all rocks, the percentage cover of filamentous and foliose algae, sessile invertebrates and the sediment matrix was assessed immediately prior to experimental manipulations and then at 2 monthly intervals for 18 months. The assessment took place in a two-stage process, using a modification of the methods of Valentine and Johnson (2003). The percentage cover of overstorey algae was estimated by using the point intercept method based on 50 equidistant points for the six fixed 0.15x0.15 m quadrats on each rock. Any algae ≥300 mm in length was designated as overstorey. The fronds of

these algae were then moved aside to allow assessment of the abundance of the understorey community.

The understorey community was assessed by photographing the six fixed 0.15x0.15 m quadrats on each rock using a digital Canon Powershot camera A95 with two-Nikonos SB-102 strobes. The percentage cover of filamentous and foliose algae, sessile invertebrates and the sediment matrix was then estimated from these photos using point intercepts. A grid of 100 equidistant points was overlaid on each photo and the organisms under each point identified. Some algae and sessile invertebrates could not be identified to species level, and it was necessary to allocate these species to species complexes or higher taxonomic groups (e.g. *Zonaria* and *Lobophora* species complex, sponge, ascidian etc).

H. rubra habitat preferences

At the beginning of the experiment, the rock dimensions (height, width and length) were measured and the rock surface area calculated as:

Area=2(lengthxwidth) + 2(lengthxheight) + 2(heightxwidth).

To quantify *H. rubra* patterns of habitat use we recorded the number of abalone on NERA and NCA and other habitats on rocks monthly, at each location and site. The percentage cover of NERA and NCA on rocks was then estimated from photographs using the methods outlined above. The surface area of rock covered by NERA and NCA and other habitat types was calculated as:

NERA and NCA area=(cover of NERA and NCAxrock area)xrock area) / rock area

Other habitat type area=(rock area – area of NERA and NCA)xrock area / rock area

To test *H. rubra* behavioural preferences for particular habitat types at the end of the 18 month experimental period (summer 2006), 10 extra rocks at each site at Maria Island and 6 extra rocks at each site at George Third Rock were selected randomly. All rocks supported ≥3 *H. rubra.* On each rock, 3 homescars were marked using the methods outlined above. The behaviour of abalone subject to the following treatments was then observed (using n=5

replicates of each treatment at Maria Island and n=3 replicates of each treatment, at each site at George Third Rock):

Treatment 1: rocks with 3 tagged *H. rubra,* undisturbed and sitting on their homescars;

Treatment 2: rocks with 3 tagged *H. rubra,* removed from and immediately returned to their original homescars;

Treatment 3: rocks with 3 tagged *H. rubra,* removed from their original homescars on other rocks and transplanted onto new homescars the experimental rocks;

Treatment 4: 3 tagged *H. rubra* removed from their original homescars on other rocks and placed onto 3 overgrown homescars on experimental rocks.

All *H. rubra* were tagged with an orange crayon. The number and position of tagged *H. rubra* was assessed on the first day of the manipulation and again after one week.

Analysis

Number of *H. rubra*

At both locations, the effectiveness of our experimental removals of *H. rubra* was assessed as the difference in the initial number of abalone on rocks (immediately prior to manipulations) and the final number of abalone on rocks (18 months after commencing experimental manipulations), (i.e. initial – final).

At Maria Island, the effect of removals on the difference in the total number of *H. rubra* was analysed using 2-way mixed effects ANOVA. The model included the fixed effects of treatment (2 levels, control and removal) and the random effect of site (2 levels, Jetty and Magistrate's Point) and their interaction.

At George Third Rock, the effectiveness of our removals of *H. rubra* was also analysed using a 2-way mixed effects ANOVA. The model included the fixed effects of treatment (4 levels, unmanipulated *H. rubra* on unfenced rocks and unmanipulated *H. rubra* on partially fenced rocks, removal of *H. rubra* from unfenced rocks and removal of *H. rubra* from fenced rocks) and the random effect of sites (2 levels, SE and SW) and their interaction. Where

significant differences between treatments were found planned comparisons were made. For non-orthogonal contrast, the significance level was adjusted using the methods of Todd & Keough (1994).

To test the effect of the fences:

Contrast 1: unmanipulated *H. rubra* on unfenced rocks vs. unmanipulated *H. rubra* on partially fenced rocks

To test the effect of partial removals of *H. rubra:*

Contrast 2: unmanipulated *H. rubra* on unfenced rocks vs. removal of *H. rubra* from unfenced rocks

To test the effects of complete removals of *H. rubra:*

Contrast 3: unmanipulated *H. rubra* on unfenced rocks vs. removal of *H. rubra* from fenced rocks

To test difference between partial and complete removals of *H. rubra:*

Contrast 4: removal of *H. rubra* from unfenced rocks vs. removal of *H. rubra* from fenced rocks

Effect of removing *H. rubra* on benthic community structure

For Maria Island, the effects of removing *H. rubra* on benthic community structure were analysed using a 3-way mixed effects split plot PERMANOVA model. The model included the main effects of treatment (fixed; 2 levels, removal and control), sites (random; 2 levels, Jetty and Magistrate's Point), rock nested within treatment and site (random; 5 levels, rocks), and the split plot effect of position on the rock (fixed; 2 levels, homescars and other positions on the rock) and their interaction. Similarly, the effect of removing *H. rubra* on the cover of overstorey algae, NERA, NCA, filamentous and foliose algae, sessile invertebrates, and the sediment matrix was analysed using a 3-way mixed effects split plot ANOVA, of identical structure to that just described.

For George Third Rock, the effects of removing *H. rubra* benthic community structure were analysed using a 3-way mixed effects split plot PERMANOVA. The model included the main effects of treatment (fixed; 4 levels unmanipulated *H. rubra* on unfenced rocks and unmanipulated *H. rubra* on partially fenced rocks, removal of *H. rubra* from unfenced rocks and removal of *H. rubra* from fenced rocks), sites (random; 2 levels, SE and SW), rock nested within treatment and site (random; 3 levels, rocks) and the split effect of position on the rock (fixed; 2 levels, homescars and other

positions on the rock) and their interaction. Similarly, the effect of removing *H. rubra* on individual components of the benthos, i.e. on the cover of overstorey algae, NERA, NCA, filamentous and foliose algae, sessile invertebrates and sediment matrix was analysed using a 3-way mixed effect split plot ANOVAs and planned comparisons were made as outlined earlier.

All analyses of benthic community structure were undertaken on data collected at the end of the experiments, after 18 months of maintaining the experimental manipulations. Non-metric multidimensional scaling (nMDS) based on Bray Curtis distances was used to produce 2-dimensional representations of similarities between treatments. The Bray-Curtis similarity matrices and nMDS analyses were derived from percentage cover data after a square root transformation to reduce the influence of dominant species and undertaken using the PIMER 6.0 software.

H. rubra habitat preferences

H. rubra patterns of habitat use were analysed by comparing the observed number of abalone on each habitat type relatively to the number of abalone expected to be on each habitat type based on its surface area, using G-tests (Sokal & Rohlf 1995). The expected number of abalone on each habitat type was calculated as:

Expected number of abalone on each habitat type=(habitat area/ rock area) x10

All habitat-specific observed and expected values were analysed separately in winter and summer, (0 and 18 months), at each location (George Third Rock and Maria Island) and site (SW, SE, Magistrate's Point and Jetty) and the Bonferroni correction was used to adjust for multiple comparisons.

To identify which habitat types were responsible for significant differences in *H. rubra* proportional habitat use we calculated monthly habitat association indices for both locations and all sites. Indices ranged between >0.5 (preference for NERA and NCA) to <0.5 (preference for other habitat types) with 0 representing neutral association, using the equation:

Habitat association=(number of *H. rubra* on NERA and NCA /area of NERA and NCA) / (number of *H. rubra* on NERA and NCA/ area of NERA and NCA) + (number of *H. rubra* on other habitat types/ area of other habitat types)

The proportion of *H. rubra* resighted on homescars through time (days) were analysed using 3-way mixed effect ANOVA. The model included the main effects of treatment (fixed; 4 levels=*H. rubra* sitting on homescars, undisturbed; *H. rubra* removed from and then immediately returned to their original homescars; *H. rubra* removed from homescars and placed onto new homescars on different rocks; and *H. rubra* were removed from homescars and placed onto overgrown homescars on different rocks), site (random; 2 levels, Maria Island=Jetty and Magistrate's Point; George Third Rock=SE and SE), and rocks nested within treatment and site (random, Maria Island=5 levels, rocks; George Third Rock=3 levels, rocks), and all interactions. Where significant differences were found planned comparisons were made. For non-orthogonal contrast, the significance level was adjusted using the approach of Todd and Keough (1994). Planned comparisons were:

To test the effect of the transplant procedure on the proportion of tagged *H. rubra* on their homescars:

Contrast 1: control, undisturbed *H. rubra* sitting on homescars vs. *H. rubra* removed from and then immediately returned to their original homescars

To test the effect of being transferring abalone to another homescar on different rocks on the proportion of tagged *H. rubra* on their homescars

Contrast 2: control vs. *H. rubra* were removed from homescars and placed onto new homescars on different rocks

To test the effect of overgrown homescars on the proportion of tagged *H. rubra* found on their homescars:

Contrast 3: control vs. *H. rubra* removed from homescars and placed onto overgrown homescars on different rocks

For all parametric analyses, the relationship between standard deviation and means of treatment groups was used to determine the appropriate transformation to stabilize variances, and transformed data were checked for both normality (using normal probability plots) and homoscedasticity. Variables that were transformed are expressed in terms of the untransformed variable *Y*. All univariate statistical analyses and graphics were produced using the R statistical software.

RESULTS

Effect of removing *Haliotis rubra* on the total number of abalone on rocks

At Maria Island, very few abalone reinvaded rocks initially cleared of *H. rubra* (Figure 1, Table 1). By the end of the experiment, there was a much greater number of *H. rubra* on control rocks than on the rocks from which abalone were removed (Figure 2, Table 1).

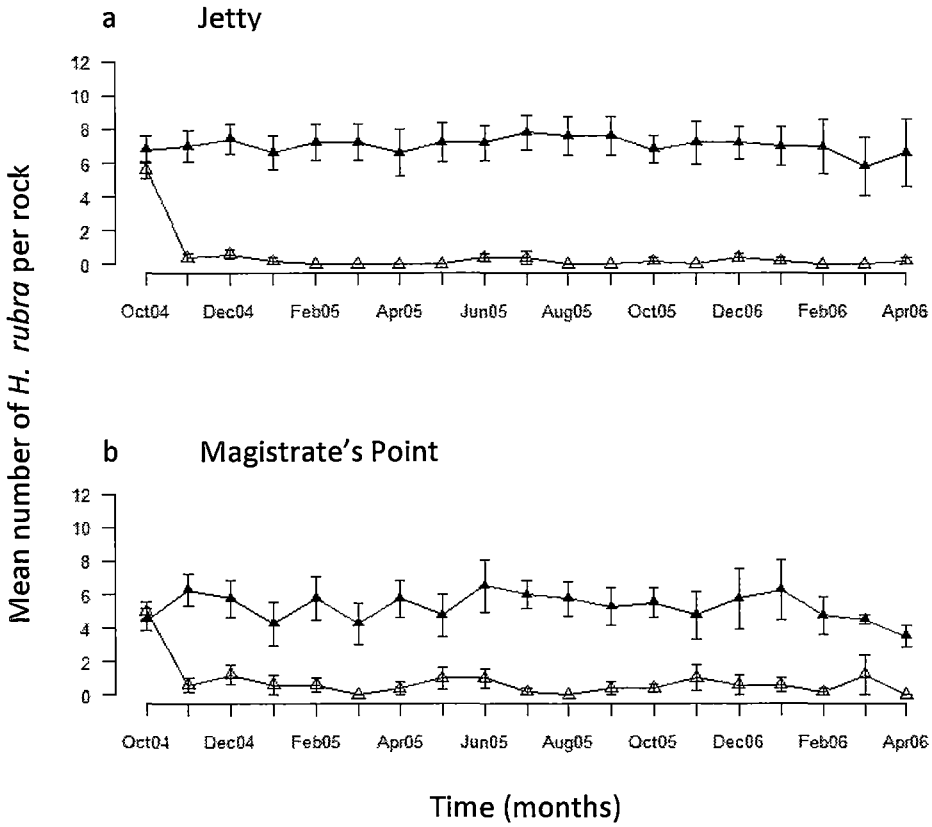

Figure 2. Mean number of abalone per rock (+/- SE) in experimental treatments (n=5) through time (months) at (a) Jetty and (b) Magistrate's Point, Maria Island. Treatments are, black triangles=unmanipulated *H. rubra*, white triangles=removal of *H. rubra*, (see Table 1 ANOVA results).

In contrast, at George Third Rock, abalone were ostensibly more mobile (Figure 2, Table 1). While very few *H. rubra* reinvaded the fenced rocks from which abalone were removed, they readily recolonised the unfenced rocks between monthly visits (Figure 2). There were no detectable effects of the fences on abalone behaviour (Table 1). Our removals of *H. rubra* were

effective in maintaining a lower total number of abalone in removal treatments than in the control (Table 1). Although some *H. rubra* recolonised the unfenced rocks from which abalone were removed, by 18 months there were no detectable differences in the difference in the total number of abalone on the fenced and unfenced rocks from which *H. rubra* were removed (Table 1). While these patterns were broadly consistent between treatments there were more abalone in the fenced and unfenced control rocks at the SW than at the SE site (Figure 2).

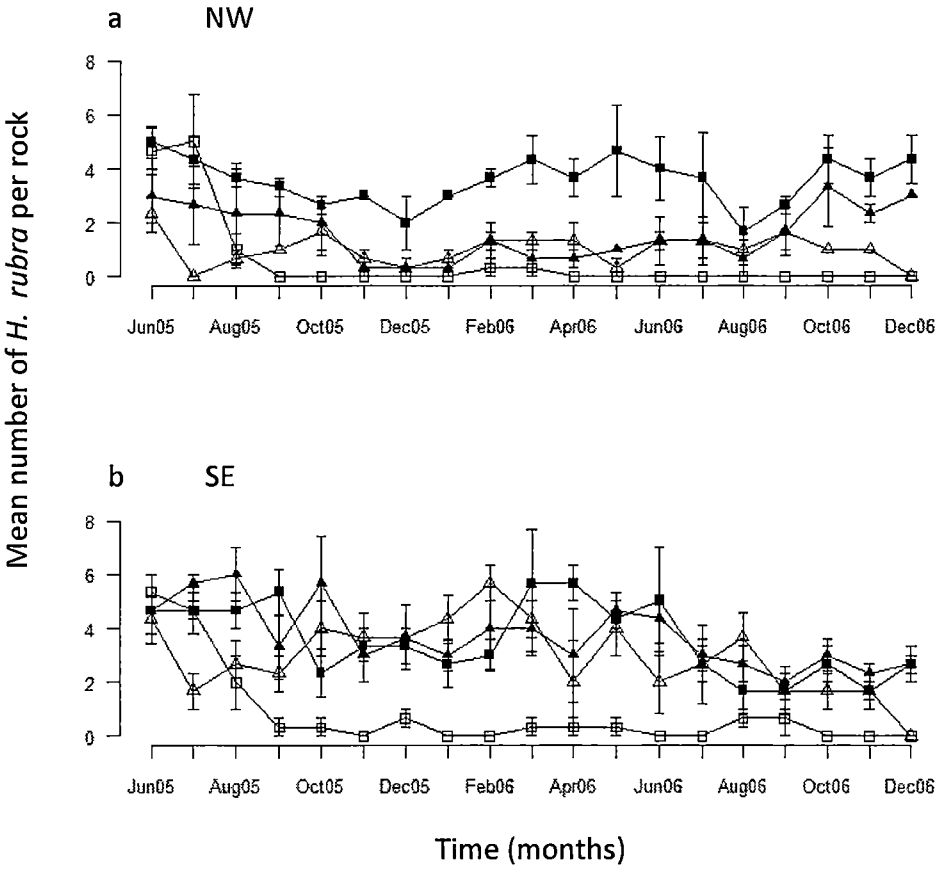

Figure 3. Mean number of abalone per rock (+/- SE) in the experimental treatments (n=3) through time (months) at (a) SW and (b) SE, George Third Rock. Treatments are, black triangles=unmanipulated *H. rubra* on unfenced rocks, black squares=unmanipulated *H. rubra* on partially fenced rocks, white triangles=removal of *H. rubra* from unfenced rocks, white squares=removal of *H. rubra* from fenced rocks, (see Table 1 ANOVA results).

Table 1. *Haliotis rubra.* Results of ANOVAs and planned comparisons (George Third Rock only), testing the effects of removing *H. rubra* on the number of abalone on rocks 2 locations, 18 months after initial experimental manipulations. Treatment codes are T1=unmanipulated *H. rubra* on unfenced rocks, T2=unmanipulated *H. rubra* on partially fenced rocks, T3=removal of *H. rubra* from unfenced rocks, and T4=removal of *H. rubra* from fenced rocks. Significant p-values are shown in bold print: $p<0.05$ are significant from the main analysis and $p<0.025$ values are significant for comparisons (α-adjusted using the method of Todd & Keough 1994).

Factors	**df**	**MS**	***F***	**p**	**Planned Comparisons**	***F***	**p**
Maria Island							
Treatment	1	115.804	12.68	**0.002**			
Site	1	0.11	0.01	0.17			
Treatment x Site	1	3.81	0.42	0.25			
Rock (Treatment x Site)	4	2.08	0.23	0.09			
Error	11	9.14					
George Third Rock							
Treatment	3	30	11.456	**0.02**	T1 vs.T2	1.081	0.323
Site	1	13.5	5.153	0.453	T1 vs.T3	289	**$1e^{-5}$**
Treatment x Site	3	0.033	0.013	**0.04**	T1 vs.T4	289	**$1e^{-8}$**
Rock (Treatment x Site)	8	10.044	3.836	0.07	T3 vs.T4	1.76	0.62
Error	8						

Effect of removing *H. rubra* on benthic habitat structure

At the beginning of the experiment at Maria Island, the benthic community structure on homescars differed significantly to that at other positions on rocks (Figure 4, Table 2). There were also significant differences in the benthic community structure between sites and rocks within locations (Table 2). At the conclusion of the experiment (18 months after initial removals), there was clear separation in MDS space in the community associated with homescars on control rocks with abalone, and on homescars on rocks from which *H. rubra* had been removed (Figure 4). Although the distinction was not as marked, there was also separation in MDS space in community structure at positions away from the homescars between control and removal treatments (Figure 4). While these trends were broadly consistent between treatments there were also differences in the benthic community structure between rocks (Table 2).

In contrast, at the beginning of the experiment the benthic community structure on homescars and other position on all rocks at George Third Rock was very similar (Figure 4, Table 2). There were however significant differences in the benthic community structure between the rocks (Table 2). After eighteen months of applying, the treatments there were distinct differences in community composition between treatments (Table 2). The community structure in the control, (unmanipulated *H. rubra* on unfenced rocks) and the treatment of unmanipulated *H. rubra* on partially fenced rocks was similar, suggesting there was no effect of fences on benthic community structure (Table 2). Similarly, there was very little difference in MDS space between the control, and the treatment in which abalone was removed from unfenced rocks (Figure 4). There were however, distinct differences between the control, and between the unfenced and fenced treatments in which *H. rubra* were removed (Figure 4).

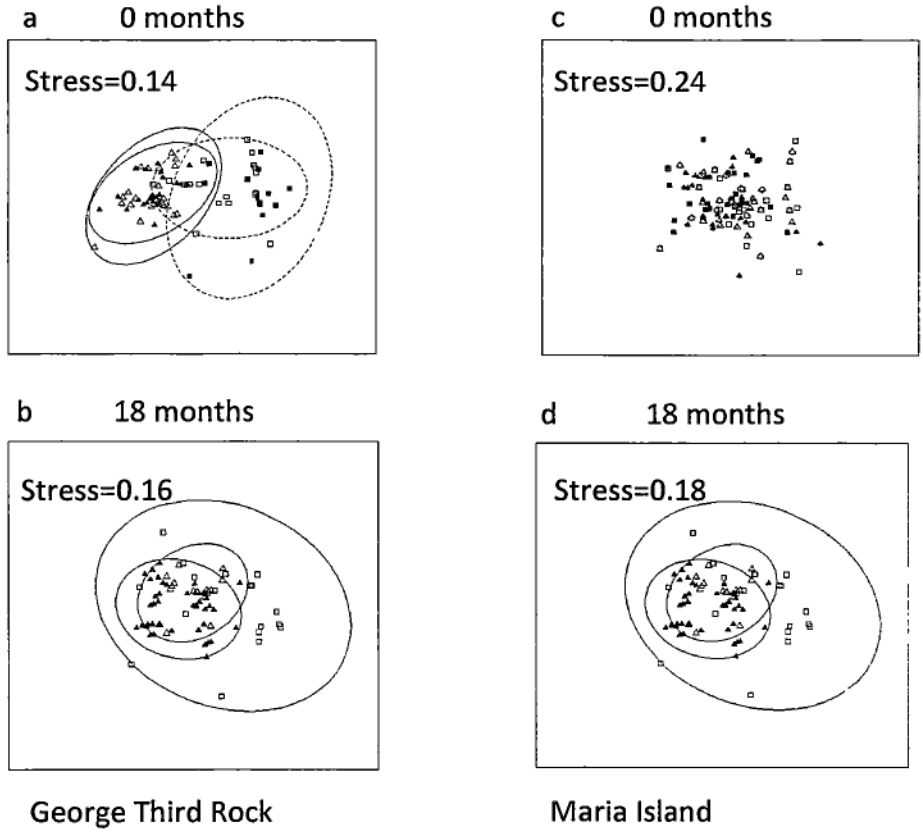

Figure 4. Ordination (nMDS) of benthic community structure on homescars (triangles) and at other randomly selected positions (squares) on the rocks in treatments from *H. rubra* were removed from rocks (white symbols) or unmanipulated (black symbols) (a) immediately before manipulations and (b) 18 months after, at Maria Island, (c) all treatments immediately before manipulations, (unmanipulated *H. rubra* on unfenced rocks black triangles, unmanipulated *H. rubra* on partially fenced rocks black squares, removal of *H. rubra* from unfenced rocks white triangles and removal of *H. rubra* from fenced rocks white squares) and for (d) 3 treatments (unmanipulated *H. rubra* on unfenced rocks, removal of *H. rubra* from unfenced rocks and removal of *H. rubra* from fenced rocks) 18 months after, at George Third Rock. Symbols are individual quadrats. Ordinations were based on Bray-Curtis similarity matrices of square root transformed cover data (see Table 2 PERMANOVA results). Ellipses have been drawn around treatments in (c) and (d) for clarity.

Table 2. Benthic community structure. Results of PERMOVAs and planned comparisons (George Third Rock only) testing the effect of removing *H. rubra* on the benthic community on rocks at 2 locations assessed immediately before experimental manipulations and 18 months after. Treatment codes are T1=unmanipulated *H. rubra* on unfenced rocks, T2=unmanipulated *H. rubra* on partially fenced rocks, T3=removal of *H. rubra* from unfenced rocks, and T4=removal of *H. rubra* from fenced rocks. Position refers to homescars or other areas on rocks, while treatment refers to the effect of removing abalone. Significant p-values are shown in bold print: $p<0.05$ are significant from the main analysis and $p<0.025$ values are significant for comparisons (α-adjusted using the method of Todd & Keough (1994)).

Factors	df	MS	*F*	p	Planned Comparisons	*T*	p
Maria Island							
0 months							
Treatment	3	1911.26	2	0.28			
Site	1	3088.02	5.31	**0.01**			
Treatment x Site	3	959.35	1.65	0.2			
Rock (Treatment x Site)	16	581.78	1.92	**0.02**			
Position	1	40391.14	62.52	**0.009**			
Position x Treatment	3	827.63	0.81	0.47			
Position x Site	1	646	1.8	0.19			
Position x Treatment x Site	3	1021.75	2.85	0.11			
Position x Rock (Treatment x Site)	16	358.91	1.18	0.25			
Error	96						
18 months							
Treatment	1	154993.61	68.71	**0.002**			
Site	1	3419.79	2.09	0.13			
Treatment x Site	1	2255.96	1.38	0.23			
Rock (Treatment x Site)	16	1637.41	2.3	**0.001**			
Position	1	6588.17	9.14	**0.001**			

Position x Treatment	1	4917.24	23.26	**0.02**			
Position x Site	1	720.66	0.71	0.48			
Position x Treatment x Site	1	211.44	0.21	0.89			
Position x Rock (Treatment x Site)	16	1017.8	1.43	0.08			
Error	80						
George Third Rock							
0 months							
Treatment	3	4322.18	2.25	0.1			
Site	1	337.7	0.29	0.89			
Treatment x Site	1	1919.7	1.64	0.092			
Rock (Treatment x Site)	16	1171.76	1.964	**0.001**			
Position	1	3306.04	4.497	0.35			
Position x Treatment	3	1195.506	2.258	0.081			
Position x Site	1	735.25	0.585	0.71			
Position x Treatment x Site	3	735.254	0.422	0.95			
Position x Rock (Treatment x Site)	16	1256.49	2.106	**0.001**			
Error	96	596.6					
18 months							
Treatment	3	19587.67	20.572	**0.001**	T1 vs. T2	2.203	0.07
Site	1	1307.877	1.466	0.213	T1 vs. T3	8.432	**0.013**
Treatment x Site	1	952.173	1.067	0.398	T1 vs. T4	3.762	**0.024**
Rock (Treatment x Site)	16	892.509	2.385	0.085	T3 vs. T4	4.401	**0.021**
Position	1	49.265	0.024	0.975			
Position x Treatment	3	1773.273	1.481	0.257			
Position x Site	1	2154.108	1.24	0.287			
Position x Treatment x Site	3	1197.415	0.689	0.75			

Position x Rock (Treatment x Site)	16	1737.802	2.501	**0.001**
Error	96			

Effect of removing *H. rubra* on benthic habitat

At both locations, removals of *H. rubra* resulted in a decline in the cover of encrusting red algae (NERA) and non-geniculate coralline algae (NCA) and an increase in the cover of the sediment matrix (semi-consolidated matrix of sediment and filamentous algae), filamentous algae, sessile invertebrates and understorey foliose algae (Figure 5, 6, 7, 8, Table 3, 4).

At George Third Rock, to test the effect of fences we compared the cover of the NERA, NCA, filamentous algae, sessile invertebrates, understorey foliose brown, green, red, and juvenile canopy-forming algae on the on control rocks with unmanipulated *H. rubra* to the partially fenced rocks with unmanipulated abalone (Table 4). There were no detectable effects of fences on the cover of NERA, NCA, filamentous algae, sessile invertebrates, understorey foliose green, red, and juvenile canopy-forming algae (Table 4). There was, however, a significantly higher cover of the sediment matrix and sessile invertebrates on partially fenced rocks with unmanipulated *H. rubra* than the control rocks (Figure 6, Table 4). The cover of the sediment matrix and sessile invertebrates in the fenced and unfenced treatments from which *H. rubra* was removed was similar which suggests that the fences obscured rather than enhanced the effects of removing abalone (Figure 6, Table 4). The overall conclusion is that fences had very little effect on the dependent variables we were measuring and results hereafter focus on the effect of removing abalone on the understorey community.

Effect of removing *H. rubra* on understorey community

At Maria Island, experimental removals of *H. rubra* resulted in a marked decline in the cover of NERA and NCA on homescars and other positions on rocks and an initial increase in the cover of sediment matrix on homescars on rocks (Figure 5). Through time however, the cover of the sediment matrix on homescars and other positions on rocks declined and there was an increase in the cover of filamentous algae (mainly red) and sessile invertebrates (Figure 5, Table 3). At the final assessment (Summer 2006) there was a significantly lower cover of NERA and NCA and the sediment matrix and a higher cover of filamentous algae and sessile invertebrates on rocks from which *H. rubra* were removed relative to control rocks where *H. rubra* were unmanipulated (Figure 5, Table 3). On control rocks the cover of NCA and particularly NERA was greater on homescars than on other positions however, differences in NCA were not always significant (Figure 5, Table 3). While these patterns were broadly consistent among sites, there was also a much higher amount of filamentous algae and sessile invertebrates on rocks at the Jetty than at Magistrate's Point.

Removals of *H. rubra* from rocks at George Third Rock also resulted in a declines in the cover of NERA and NCA, an initial increase in the cover of sediment matrix followed by filamentous algae (mainly red algae) and sessile invertebrates (Figure 6, Table 4). After eighteen months, the cover of NERA and NCA was much lower in the treatments in which *H. rubra* was removed, whether the rocks were fenced or not than in the control (Figure 6, Table 4). There was a much lower cover of filamentous algae on homescars on control rocks, than on what were previously homescars on rocks from which *H. rubra* was removed (Figure 6). However, at other positions on rocks the cover of filamentous algae and the cover of the sediment matrix on control rocks and on unfenced rocks from which *H. rubra* were removed were similar (Figure 6). The cover of sediment matrix in the control, was similar to the treatment where *H. rubra* were removed from unfenced rocks (Figure 6, Table 4). The cover of sessile invertebrates was higher in all treatments from which *H. rubra* was removed than on the control rocks (Figure 6, Table 4). There were no detectable differences in the cover of sessile invertebrates and the sediment matrix between treatments where *H. rubra* was removed (Figure 6, Table 4). While these trends were broadly consistent between treatments there were significant differences in the cover of filamentous algae, the sediment matrix and sessile invertebrates between rocks (Table 4).

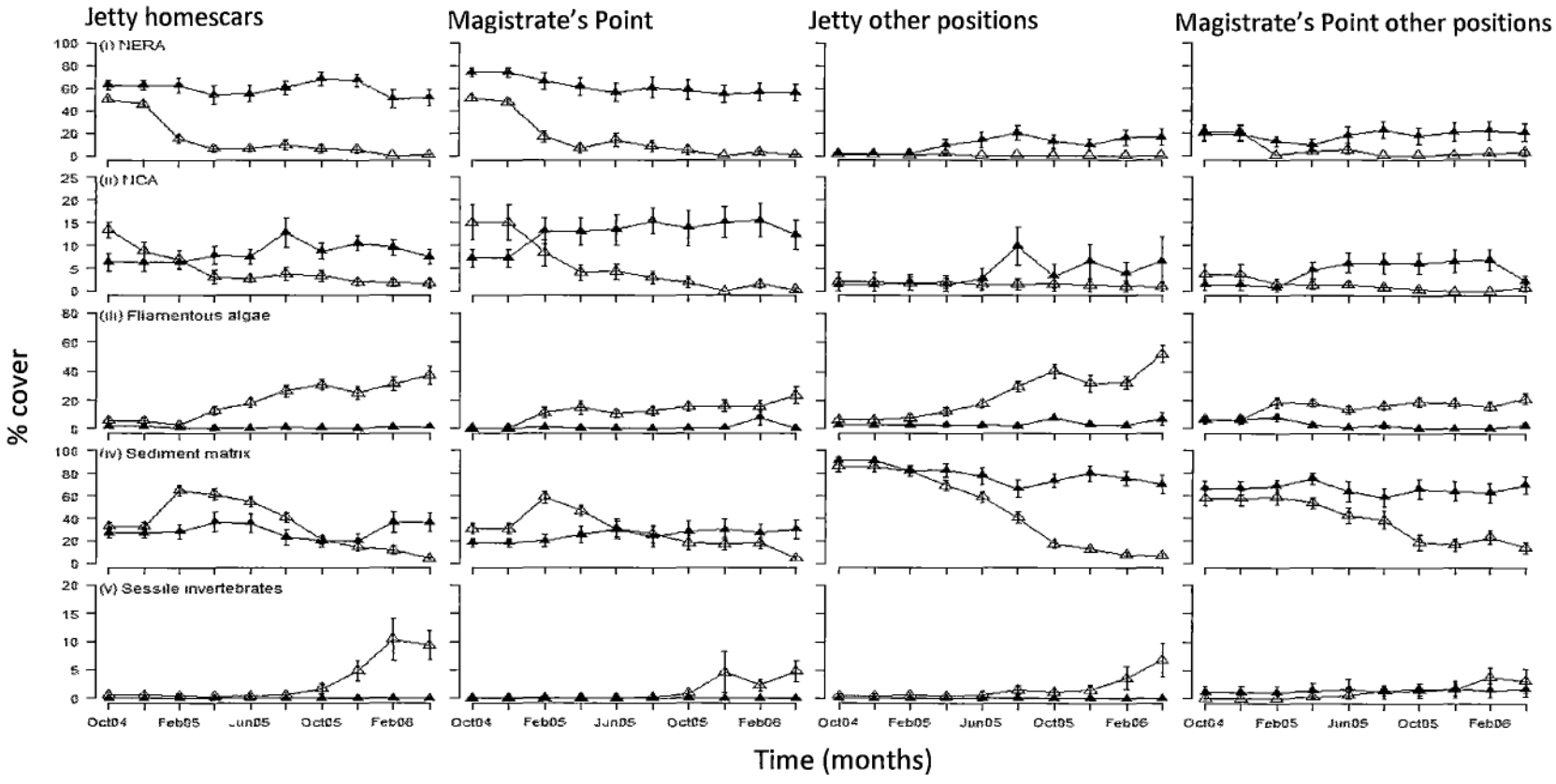

Figure 5. Mean cover (+/-SE) of (i) NERA, (ii) NCA, (iii) filamentous algae, (iv) sediment matrix, and (v) sessile invertebrates on homescars and other positions on the rocks through time (months) at the Jetty and Magistrate's Point, Maria Island in removal experiment. Treatments (*n=5*) are, black triangles=unmanipulated *H. rubra*, and white triangles=removal of *H. rubra*, (see Table 3 ANOVA results).

Table 3. Understorey community. Results of ANOVAs testing the effect of removing *H. rubra* on the cover of NERA, NCA, filamentous algae, the sediment matrix, sessile invertebrates, foliose green and red algae, understorey brown algae and juvenile canopy algae on homescars and at other positions on rocks at Maria Island, after 18 months of maintaining treatments. Significant p-values are shown in bold print ($p<0.05$).

Factors	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**
Variable	**NERA** log*Y*+0.001	**NCA**	**Filamentous algae** log*Y*+0.001	**Sediment matrix**	**Sessile Invertebrate**	**Green algae** log *Y*+0.001	**Red algae** Log *Y*+0.001	**Understorey brown** log *Y*+0.001	**Juvenile canopy** log *Y*+0.001
Treatment	1 15555.2 **0.005**	1 192.67 **0.04**	1 518.53 **0.03**	1 149.684 **0.04**	1 5.85 0.25	1 69.89 **$3e^{-7}$**	1 25.92 **0.001**	1 5.23 **0.04**	1 85.57 **$9e^{-8}$**
Site	1 0.63 0.56	1 0.03 0.13	1 2.26 0.16	1 1.36 0.451	1 3.07 0.1	1 2.4 0.14	1 0.38 0.46	1 0.2 0.34	1 2.07 0.17
Treatment x Site	1 0.005 0.06	1 0.07 0.2	1 0.23 0.36	1 148.74 **0.046**	1 7.44 **0.02**	1 3.28 0.09	1 0.38 0.46	1 0.51 0.52	1 0.05 0.18
Rock (Treatment x Site)	16 0.06 0.18	16 0.7 0.26	16 1.05 0.47	16 0.005 0.055	16 0.38 **0.03**	16 7.32 **$4e^{-10}$**	16 1.5 0.13	16 3.28 **0.002**	16 1.68 0.07
Position	1 185.86	1 1.75	1 88.21	1 1.856	1 0.99	1 1.99	1 2	1 2.75	1 4.54

		0.04	0.42	**0.05**	0.41	0.5	0.18	0.18	0.12	**0.05**
Position	x	1	1	1	1	1	1	1	1	1
Treatment		2.19	0.55	0.28	23.615	11.4	166	31.35	2.17	6.41
		0.38	0.42	0.22	0.13	0.19	**0.05**	0.11	0.4	0.24
Position	x	1	1	1	1	1	1	1	1	1
Site		0.16	0.97	0.04	0.617	0.21	0.02	1	0.07	9.05
		0.06	0.66	0.15	0.19	0.35	0.09	0.5	0.17	0.25
Position x		1	1	1	1	1	1	1	1	1
Treatment x		0.02	1.68	0.17	1.34	0.02	1.17	0.07	1.02	0.07
Site		0.11	0.28	0.32	0.29	0.11	0.3	0.2	0.33	0.19
Position	x	1	1	1	1	1	1	1	1	1
Rock		2.41	1.25	1.77	1.02	1.28	0.58	0.99	0.65	2.62
(Treatment Site)	x	**0.008**	0.26	0.06	0.45	0.24	0.11	0.52	0.17	**0.003**
Error		80	80	80	80	80				

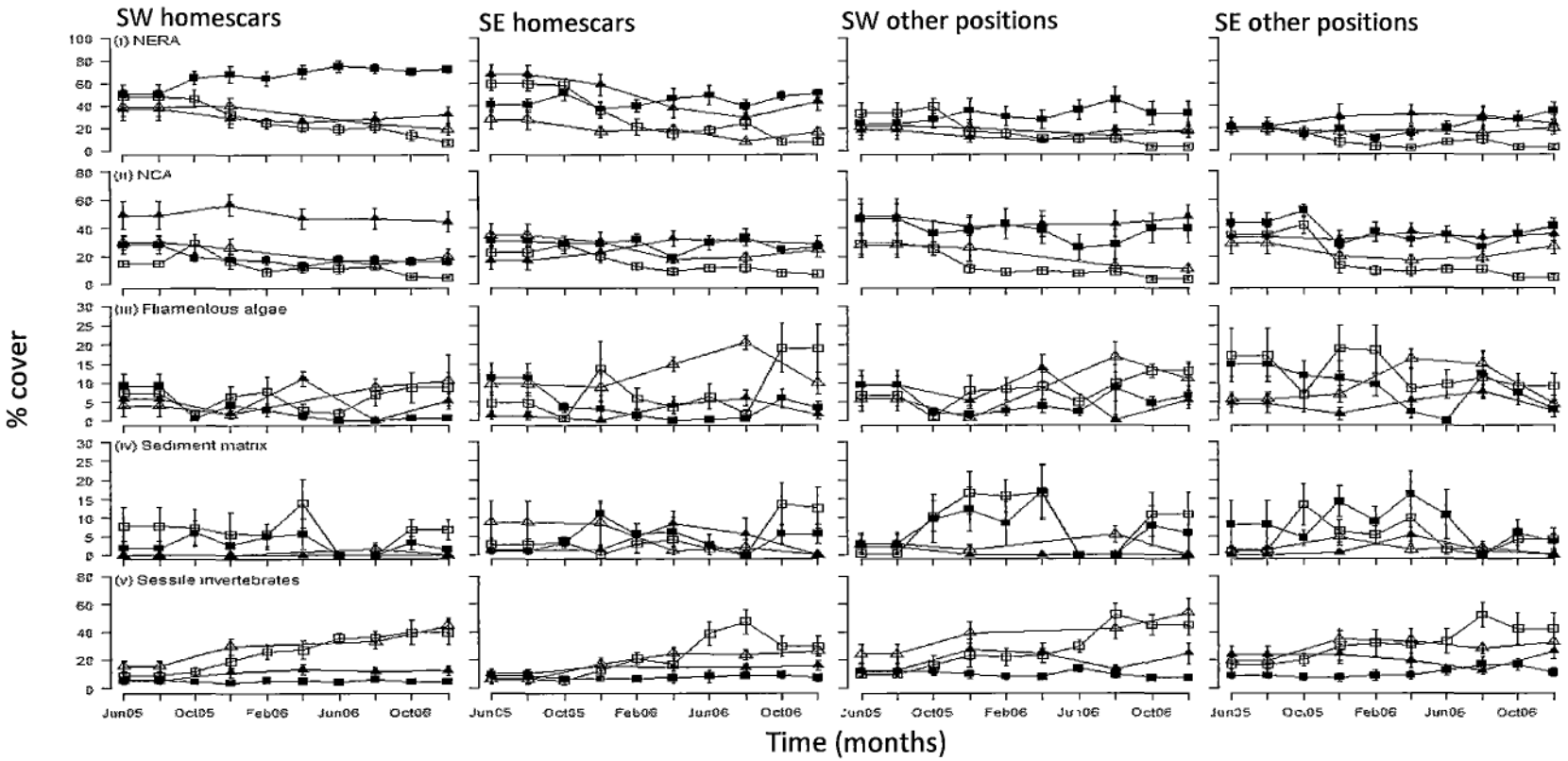

Figure 6. Mean cover (+/-SE) of (i) NERA, (ii) NCA, (iii) filamentous algae, (iv) sediment matrix and (v) sessile invertebrates on homescars and other positions on rocks through time (months) at southwest (SE) and southeast (SE), George Third Rock in removal experiment. Treatments (n=3) are, black triangles=unmanipulated *H. rubra* on unfenced rocks, white triangles=removal of *H. rubra* from unfenced rocks, black squares=unmanipulated *H. rubra* on partially fenced rocks and white

Table 4. Understorey community. Results of ANOVAs and planned comparisons testing the effect of removing *H. rubra* on the cover of NERA, NCA, filamentous algae, the sediment matrix, sessile invertebrates, foliose red algae, understorey brown algae, and juvenile canopy algae on homescars and at other positions on rocks at George Third Rock, after 18 months of maintaining treatments. Treatment codes are: T1=unmanipulated *H. rubra* on unfenced rocks, T2=unmanipulated *H. rubra* on partially fenced rocks, T3=removal of *H. rubra* from unfenced rocks, and T4=removal of *H. rubra* from fenced rocks. Significant p-values are shown in bold print: $p<0.05$ are significant from the main analysis and $p<0.025$ are significant for comparisons (α-adjusted using the method of Todd & Keough 1994).

Factors	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**
Dependent variable	**NERA** Sqrt*Y*	**NCA** Sqrt*Y*	**Filamentous algae** log*Y*+0.001	**Sediment matrix** logY+0.001	**Sessile invertebrates** sqrt*Y*	**Red algae**	**Understorey brown** $Y+0.001^{-2}$	**Juvenile canopy** $Y+0.001^{-2}$
Treatment	3	3	3	3	3	3	3	3
	56.78	14.316	2.001	48.856	11.934	10.183	0.556	19.027
	0.004	**0.03**	0.29	**0.005**	**0.036**	**0.04**	0.321	**0.019**
Site	1	1	1	1	1	1	1	1
	0.023	1.965	0.213	0.039	0.447	0.01	1.34	0.11
	0.119	0.26	0.35	0.154	0.487	0.07	0.265	0.257
Treatment x Site	1	1	1	1	1	1	1	1
	0.382	5.33	0.853	0.198	1.14	0.224	4	2.778
	0.234	0.17	0.515	0.103	0.363	0.122	**0.03**	0.075
Rock	16	16	16	16	16	16	16	16
(Treatment x Site)	1.72	0.959	2.238	2.64	2.898	1.18	0.5	0.693
	0.06	0.58	**0.009**	**0.001**	**0.001**	0.302	0.06	0.205
Position	1	1	1	1	1	1	1	1

	7	4.361	1.408	1.076	20.095	0.086	2.21	2.492
	0.078	0.33	0.321	0.375	**0.021**	0.216	**$4e^{-8}$**	0.213
Position x	3	3	3	3	3	3	3	3
Treatment	5.39	0.46	0.05	0.657	3.429	0.67	1.12	0.787
	0.305	0.5	**0.022**	0.31	0.374	0.514	**$2e^{-15}$**	0.342
Position x Site	1	1	1	1	1	1	1	1
	1.05	1.67	1.333	1.319	1	0.514	2.67	3.948
	0.38	0.15	0.298	0.334	0.61	0.475	**$4e^{-8}$**	0.141
Position x	16	16	16	16	16	16	16	16
Treatment x Site	0.589	1.07	1.333	0.527	0.09	2.14	0.38	0.904
	0.369	0.15	0.299	0.33	0.06	0.135	0.231	0.54
Position x Rock	16	16	16	16	16	16	16	16
(Treatment x Site)	0.894	0.798	1.19	1.392	1.473	0.469	1.167	0.539
	0.42	0.315	0.284	0.162	0.126	0.05	0.3	0.08
Error	96	96	96	96	96	96	96	96
Planned	***F***	***F***	***F***	***F***	***F***	***T***	***T***	***T***
Comparisons	***p***	***p***	***p***	***p***	***p***	***p***	***p***	***p***
T1 vs. T2	3.46	2.639	0.106	21.928	18.462	0.012	2.05	3.182
	0.07	0.1	0.746	**$1e^{-5}$**	**$5e^{-5}$**	0.914	0.15	0.08
T1 vs. T3	8.92	16.819	5.977	1.974	49.105	0.01	0.21	1.05
	0.003	**$1e^{-4}$**	**0.01**	0.165	**$1e^{-9}$**	0.932	0.56	0.31
T1 vs. T4	39.074	120.74	7.512	21.928	72.118	3.864	0.21	35.176
	$2e^{-5}$	**$2e^{-16}$**	**0.01**	**$1e^{-5}$**	**$2e^{-12}$**	0.04	0.65	**$1e^{-7}$**
T3. vs. T4	21.881	34.65	1.722	38.618	0.03	3.817	1.045	50.719
	$1e^{-5}$	**$1e^{-7}$**	0.194	**$3e^{-8}$**	0.961	0.04	0.31	**$8e^{-10}$**

Effect of removing *H. rubra* on foliose understorey algae

At Maria Island, between 4-6 months after the initial removals of abalone there was an increase in the cover of understorey foliose green (mainly *Caulerpa* spp.), red and brown algae (Figure 7, Table 3). Within twelve months after initiating the removals there was an increase in the cover of juvenile canopy-forming algae (mainly *Cystophora* spp.). By the end of the experiment (18 months) there was a higher cover of foliose green, red, brown and juvenile canopy-forming algae on rocks from which *H. rubra* was removed compared with the control rocks on which *H. rubra* were undisturbed (Figure 7, Table 3). In general, this pattern was consistent between rocks however there was a much higher cover of juvenile canopy-forming and foliose green algae on other positions on rocks at Magistrate's Point than at the Jetty site (Figure 7, Table 3).

At George Third Rock, eight months after the initial removals of abalone there was an increase in the cover of understorey foliose red and brown algae on these rocks relative to control rocks (Figure 8, Table 4). Through time however, the cover of foliose red and brown algae declined and there was an increase in the cover of juvenile canopy-forming algae (consisting mainly of *Phyllospora comsa*) (Figure 8, Table 4). At the conclusion of the experiment, differences in the cover of foliose red and brown algae on control rocks and in fenced and unfenced treatments where *H. rubra* were not significant (Figure 8, Table 4). In contrast, there was a higher cover of juvenile canopy-forming algae on fenced rocks from which *H. rubra* was removed than on control rocks or in the treatment where *H. rubra* was removed from unfenced rocks (Figure 8, Table 4).

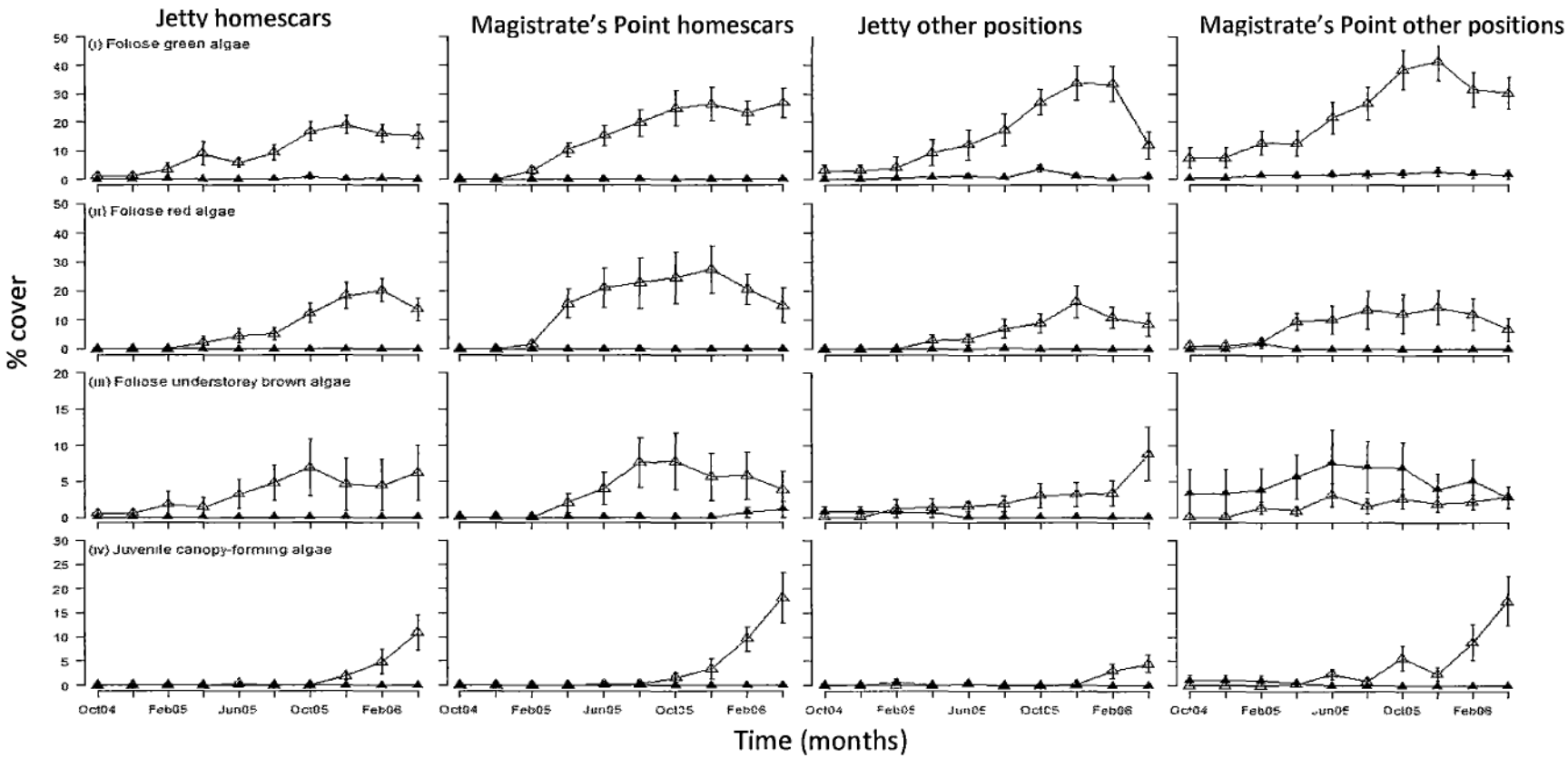

Figure 7. Mean cover (+/-SE) of (i) foliose green algae, (ii) foliose red algae, (iii) foliose understorey brown algae and (iv) juvenile canopy-forming algae on homescars and other positions on rocks through time (months) at the Jetty and Magistrate's Point at Maria Island in removal experiment. Treatments (n=5) are, black triangles=unmanipulated *H. rubra*, and white triangles=removal of *H. rubra*, (see Table 3 ANOVA results).

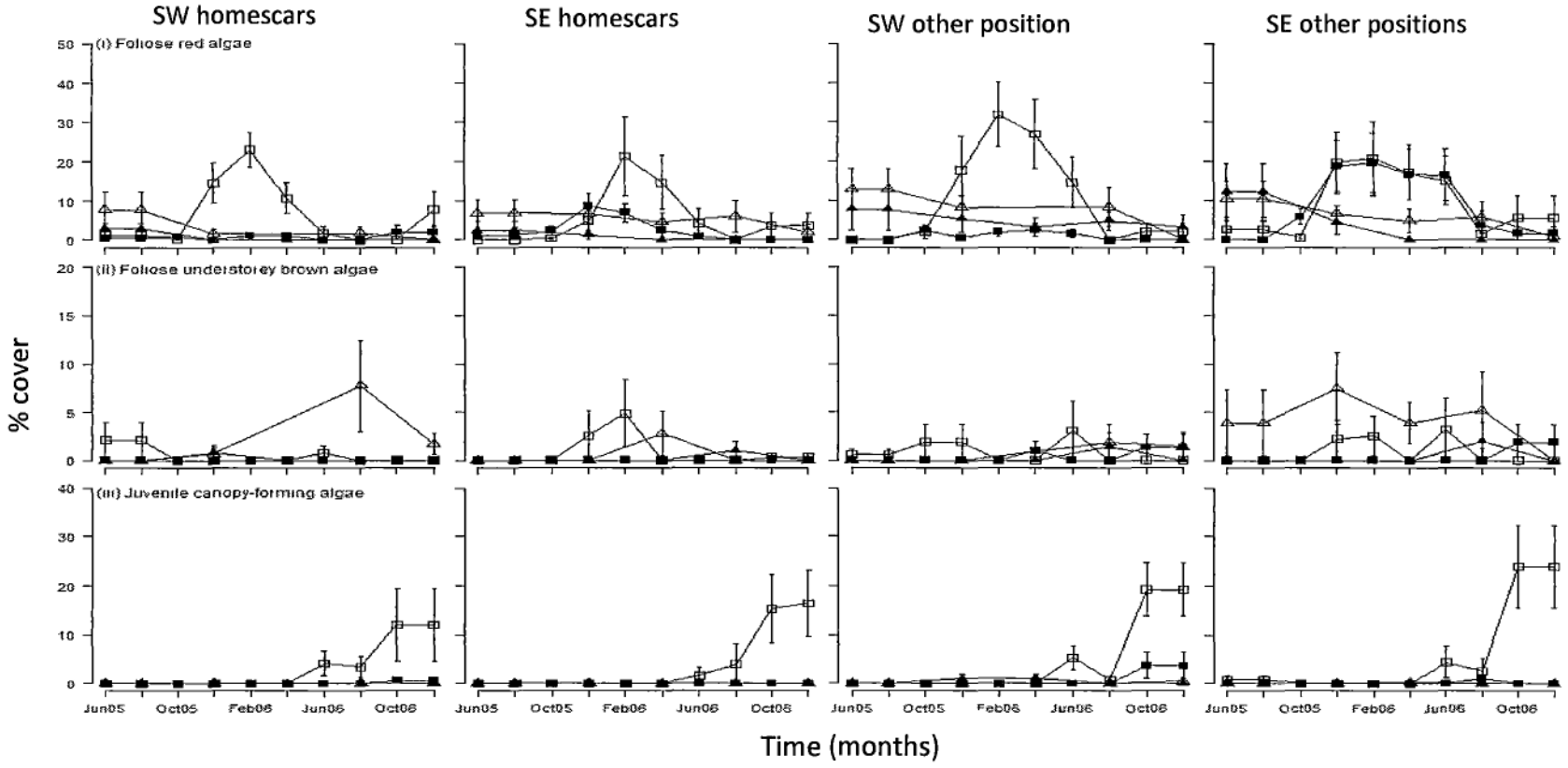

Figure 8. Mean cover (+/-SE) of (i) foliose red algae, (ii) understorey foliose brown algae and (iii) juvenile canopy-forming algae on homescars and other positions on rocks through time (months) at north-west (SE) and south-east (SE) George Third Rock in removal experiment. Treatments (*n=3*) are, black triangles=control *H. rubra* on unfenced rocks, white triangles=removal of *H. rubra* from unfenced rocks, black squares=control *H. rubra* on partially fenced rocks, and white squares=removal of *H. rubra* from fenced rocks, (see Table 4 ANOVA results).

Effect of removing *H. rubra* on overstorey algae

Throughout the experiment, the cover of overstorey algae remained consistently high on rocks at both Maria Island and George Third Rock (Table 5, 6). At the conclusion of the experiment, there were no detectable effects of removing *H. rubra* on the cover of adult *Cystophora* spp., *Ecklonia radiata* and *Sargassum* spp., at Maria Island (Table 5). There were also no detectable effects of removing *H. rubra* on the cover of adult *E. radiata, p. comsa,* and *Xiphophora gladiata* at George Third Rock (Table 6).

Table 5. Overstorey algae. Results of ANOVAs testing the effect of removing of *H. rubra* on the cover of bare rock, overstorey *Cystophera* spp., *E. radiata* and *Sargassum* spp. on homescars and at other positions on rocks at Maria Island, after 18 months of maintaining treatments. Significant p-values are shown in bold print ($p<0.05$).

Factors	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**
Dependent variable	***Cystophera* spp.** **log Y+0.001**	***E. radiata*** **$Y+0.001^{-1}$**	***Sargassum* spp.** **$Y+0.001^{-1}$**
Treatment	1	1	1
	0.06	0.09	15.98
	0.14	0.18	0.16
Site	1	1	1
	0.07	0.1	7.82
	0.16	0.19	0.22
Treatment x Site	1	1	1
	10.92	0.08	3.28
	0.19	0.18	0.22
Rock	1	1	1
(Treatment x Site)	0.34	0.8	3.28
	0.44	0.63	0.32
Position	1	1	1
	1.01	1.53	0.27
	0.34	0.24	0.4
Position x Treatment	1	1	1
	0.2	0.9	0.002
	0.27	0.48	0.2
Position x Site	1	1	1

	1.58	0.1	6.17
	0.23	0.25	0.1
Position x	1	1	1
Treatment x Site	2.44	1.18	0.5
	0.06	0.38	0.07
Position x Rock	1	1	1
(Treatment x Site)	0.69	3.7	0.5
	0.21	**$7e^{-5}$**	0.06
Error	80	80	80

Table 6. Overstorey algae. Results of ANOVAs and planned comparisons testing the effect of removing *H. rubra* on the cover of bare rock and overstorey *E. radiata, p. comsa, X. gladiata* on homescars and at other positions on rocks at George Third Rock, 18 months after experimental manipulations. Significant p-values are shown in bold print: $p<0.05$ (α - adjusted using the method of Todd & Keough (1994)).

Factors	**df** ***F*** **p**	**df** ***F*** **p**	**df** ***F*** **p**
Dependent variable	***E. radiata*** **Y+0.001^{-1}**	***p. comsa*** **Y+0.001^{-2}**	***X. gladiata*** **log Y+0.001**
Treatment	3	3	3
	7.546	0.84	4.385
	0.09	0.443	0.12
Site	1	1	1
	1.389	0.762	3.566
	0.256	0.605	0.08
Treatment x Site	1	1	1
	0.204	0.381	1.243
	0.108	0.231	0.32
Rock	16	16	16
(Treatment x Site)	0.783	0.47	0.415
	0.299	0.06	**0.02**
Position	1	1	1
	2.778	1.589	0.436
	0.194	0.297	0.444
Position x Treatment	3	3	3
	9	1.417	56.197
	0.283	0.538	0.1
Position x Site	1	1	1
	0.158	1.2	1.131
	0.283	0.354	0.366
Position x	16	16	16
Treatment x Site	1.06	0.785	0.09
	0.396	0.481	0.08
Position x Rock	16	16	16
(Treatment x Site)	0.261	0.38	0.668
	0.001	**0.016**	0.182
Error	96	96	96

H. rubra habitat use and preferences

At both locations, sites and seasons, *H. rubra* did not use the habitat types on rocks in proportion to its availability (Figure 9, Table 6). Throughout the experiment, there were significantly more *H. rubra* than expected on NERA and NCA and significantly fewer abalone than expected on other habitats on rocks (Table 6).*H.HH* The proportion of *H. rubra* on NERA and NCA varied widely each month, suggesting that abalone move between areas of NERA and NCA and that this is their preferred habitat type (Figure 9, Table 6).

Table 6. *Haliotis rubra.* Results of G-tests testing *H. rubra* habitat use relative to its availability on rocks at two locations Maria Island and George Third Rock, four sites Magistrate's Point, Jetty, southwest (SW) and southeast (SE), in winter and summer (0 and 18 months after experimental manipulations). Significant p-values are shown in bold print: $p<0.006$ (α-adjusted using the Bonferroni method).

	Winter (0 months)			**Summer (18 months)**		
Factors	**df**	***G***	**p**	**df**	***G***	**p**
Maria Island						
Magistrate's Point	9	81.843	**$7e^{-14}$**	9	72.245	**5.5e-12**
Jetty	9	73.855	**$2.5e^{-13}$**	9	48.224	**3.2e-8**
George Third Rock						
SW	11	48.224	**$3.2e^{-8}$**	11	102.665	**2e-16**
SE	11	48.082	**$1.4e^{-6}$**	11	46.467	**2e-6**

The proportion of *H. rubra* resighted after 1 and 7 days differed between the treatments (Figure 10, Table 7). There was a lower proportion of *H. rubra* found on overgrown homescars after day 1 and 7 compared with the control, where abalone were left undisturbed on homescars (Figure 10, Table 7). There were no detectable differences in the proportion of *H. rubra* occupying homescars in the treatments where abalone were removed and replaced on the same homescar; where abalone were removed and replaced on different homescars on different rocks; and the control where abalone were left undisturbed on homescars (Figure 10, Table 7). These results were consistent between sites and locations (Table 7).

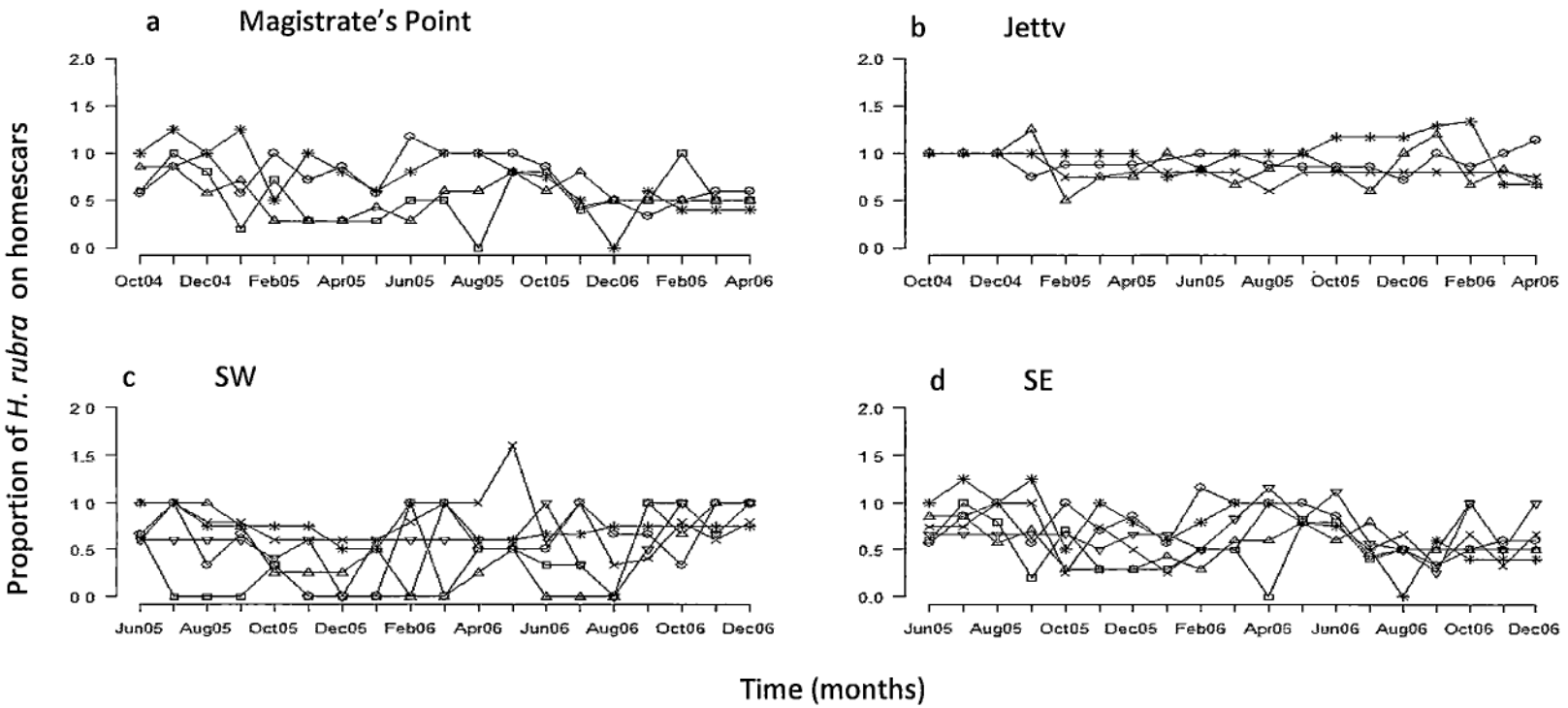

Figure 9. Proportion of homescars occupied by *H. rubra* on individual rocks through time (months) at (a) Magistrate's Point and the (b) Jetty at Maria Island and SW and SE George Third Rock. Data are individual rocks (n=6 at George Third Rock and n=5 at Maria Island). Treatments are Treatments (n=3) are, black triangles=control *H. rubra* on unfenced rocks, white triangles=removal of *H. rubra* from unfenced rocks, black squares=control *H. rubra* on partially fenced rocks, and white squares=removal of *H. rubra* from fenced rocks.

Table 7. *Haliotis rubra.* Results of ANOVAs and planned comparisons testing the effects of treatments on the proportion of abalone through time (1 and 7 days) at 2 locations. Treatment codes are: T1=undisturbed *H. rubra* sitting on tagged homescars, T2=tagged *H. rubra* removed and immediately returned to their original homescars, T3=tagged *H. rubra* removed from homescars and placed onto new homescars on different rocks, T4=tagged *H. rubra* removed from homescars and placed onto overgrown homescars on different rocks. Significant p-values are shown in bold print: $p<0.05$ are significant for the main analysis and $p<0.008$ are significant for the planned comparisons (α-adjusted using the method of Todd and Keough (1994)).

Factors	**df**	**MS**	***F***	**p**	**Comparisons**	***F***	**p**
Maria Island							
1 day							
Treatment	3	2.492	107.7	**$<2e^{-16}$**	T1 vs. T2	1	0.33
Site	1	0.032	1.369	0.249	T1 vs. T3	1.106	0.31
Treatment x Site	3	0.007	0.274	0.845	T1 vs. T4	36.506	**$1e^{-5}$**
Treatment x Site (Rock)	32	0.042	1.82	**0.03**			
Error	41	0.023					
7 day							
Treatment	3	2.492	107.703	**$2e^{-4}$**	T1 vs. T2	0.764	0.394
Site	1	0.032	1.368	0.61	T1 vs. T3	1.972	0.178
Treatment x Site	3	0.007	0.274	0.16	T1 vs. T4	71.517	**$1e^{-7}$**
Treatment x Site (Rock)	32	0.042	1.819	**0.04**			
Error	41	0.023					
George Third Rock							
1 day							
Treatment	3	3.143	194.8	**$4e^{-5}$**	T1 vs. T2	1.106	0.306
Site	1	0.001	0.02	0.112	T1 vs. T3	1	0.33
Treatment x Site	3	0.041	0.84	0.519	T1 vs. T4	123.6	**$1.7e^{-9}$**
Treatment x Site (Rock)	32	0.021	1.331	0.193			

Error	41	0.016					
7 day							
Treatment	3	3.14	194.84	**$<2e^{-16}$**	T1 vs. T2	1	0.33
Site	1	0.002	0.03	0.88	T1 vs. T3	1	0.33
Treatment x Site	3	0.022	0.84	0.49	T1 vs. T4	141.51	**$5.8e^{-10}$**
Treatment x Site (Rock)	32	0.013	1.34	0.19			
Error	41						

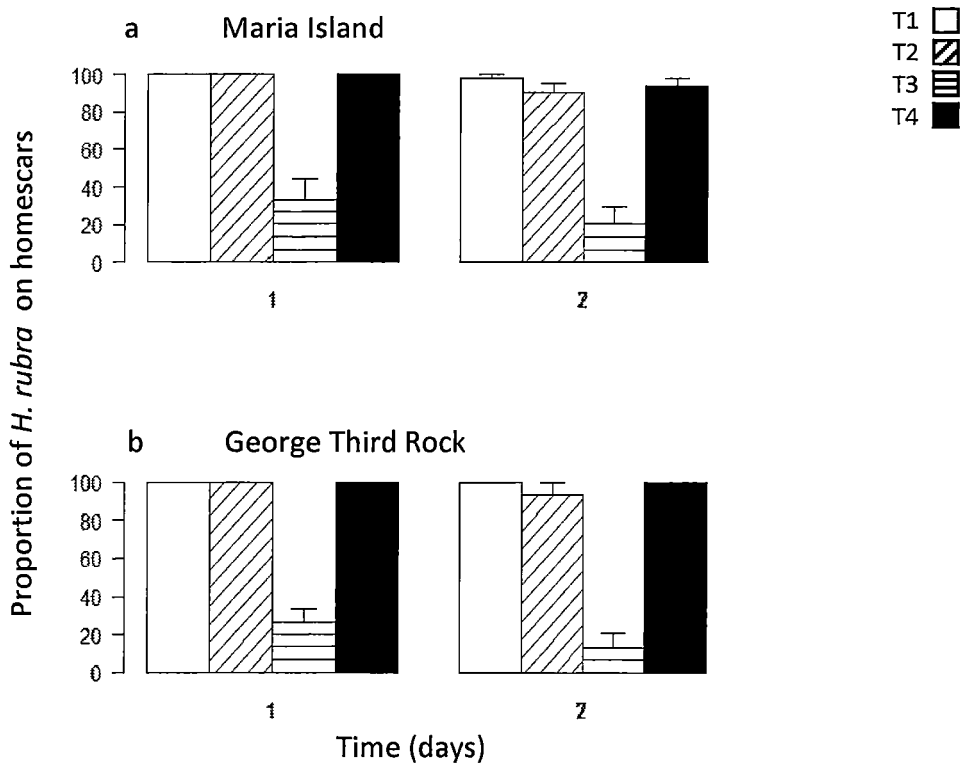

Figure 10. Mean percentage of *H. rubra* (+/-SE) on homescars at two sites at (a) Maria Island and (b) George Third Rock 1 and 7 days after experimental manipulations. Treatments are white squares=unmanipulated *H. rubra* sitting on active homescars, diagonal hatch=removal and transplant of *H. rubra* onto new homescars, horizontal hatch=transplanting *H. rubra* onto overgrown homescars, and solid squares=removal of *H. rubra* and then replacing onto the same homescar. Data are means (+/- SE) of n=5 replicates at Maria Island and n=3 replicates at George Third Rock for each treatment (see Table 9 ANOVA results).

DISCUSSION

Simulated intensive fishing of blacklip abalone (*Haliotis rubra*) led to a dramatic shift in benthic community structure on the east coast of Tasmania, Australia. Experimental removals of *H. rubra* resulted in a decline in the cover of non-calcareous encrusting red algae (NERA, *Peyssonnelia* spp. and *Hildenbrandia* spp.) and non-geniculate coralline algae (NCA) which, in turn, lead to the development of a benthic community dominated by sessile

invertebrates, filamentous and foliose algae (red, green and juvenile canopy-forming algae), the sediment matrix and sessile invertebrates that was less suitable for adult abalone. The resultant positive feedback suggests that heavy fishing of abalone could result in the benthos shifting to an alternative configuration at local scales that is poorly conducive to abalone. This habitat shift could help to explain and collapse and non-recovery of abalone stocks in areas on the east coast of Tasmania and worldwide (Jackson et al. 2001, Jenkins 2004, Miner et al. 2007).

Scale-dependent effects of fishing abalone

Marine consumers can play an important role in influencing the structure and function of the benthic habitat in many marine ecosystems (Steneck 1986, Tegner & Dayton 1999, Jackson et al. 2001, Steneck et al. 2002, Mumby et al. 2007). Similarly, our results suggested that *H. rubra* activities are important in structuring the temperate rocky reef benthic habitat on the east coast of Tasmania. Removals of *H. rubra* resulted in changes to the benthic community on both abalone homescars and elsewhere on the experimental rocks. Within two months of removing abalone, there were declines in the cover of NERA and NCA. These changes were accompanied by increases in the cover of filamentous and foliose algae, sessile invertebrates, and the sediment matrix. At the conclusion of the experiment, the rocks were covered in this alternative benthic community which is distinctly different to that dominated by NERA and NCA.

These trends were consistent across all sites and at both locations, however, there were substantial spatial and temporal differences in the detailed phenology and composition of the community that developed in response to removals of abalone. At the more sheltered location, the benthic community responded quickly to removal of *H. rubra*. Within six months of initiating abalone removals, there were increases in the cover of filamentous algae (primarily red algae) and the accumulated sediment matrix, which was gradually replaced by understorey foliose green and red algae, juvenile canopy-forming algae and sessile invertebrates. In contrast, at the more exposed location, the benthic community responded more slowly to our manipulations. It was six to eight months after the initial removal of abalone before there were notable increases in the cover of filamentous and foliose red algae, which was gradually replaced by sessile invertebrates and juvenile canopy-forming algae. The slower response may be the result of the sweeping action of overstorey algae across the substratum in surge, restricting development of understorey algae and sessile invertebrates, as has

been reported elsewhere (Velimirov & Griffiths 1979, Kennelly 1989, Connell 2003). Alternatively, it may reflect the greater depths and thus lower light levels at this location (~21 m at George Third Rock as opposed to 9 m at Maria Island). Regardless, the important result is that intensive fishing of abalone results in a shift in the benthic community structure at a range of sites and locations.

These results are consistent with surveys on the east coast of Tasmania (Valentine et al. 2009, Chapter 5), elsewhere in Australia (Shepherd 1973, Shepherd and Turner 1985, Daume et al. 1997), and worldwide including, California, U.S.A (Kitting 1997, Miner et al. 2007), British Columbia, Canada (Lessard & Campbell 2007) and South Africa (Day & Branch 2000). Previous surveys have demonstrated a positive relationship between densities of abalone and substratum covered in NERA and NCA, and a negative correlation between densities of abalone and filamentous and foliose red algae, sediment and sessile invertebrates, at a range of spatial scales (0.25x0.25 m to 25x 25 m quadrats) and depths (3-21 m), (Shepherd 1973, Shepherd & Turner 1985, Daume et al. 1997, Kitting 1997, Day & Branch 2000, Lessard & Campbell 2007, Miner et al. 2007, Valentine et al. 2009, Chapter 5). The combined research suggests intensive harvesting of abalone will result small-scale changes to the benthic habitat, however where the harvesting effort is sufficiently to reduce the densities of abalone at a larger scales it seems likely that there will be broader scale changes to the benthic community structure (Miner et al. 2007, Valentine et al. 2009, Chapter 5).

The susceptibility of algae to abalone activities was influenced by its size and toughness relative to the abalone body plan (Steneck & Watling 1982, Padilla 1985, 2004). While removing *H. rubra* resulted in significant changes to the understorey, there were no detectable effects of removing abalone on the cover of the established overstorey algae. However, at the conclusion of the experiment (eighteen months after the initial removal of abalone from rocks), in the treatments where *H. rubra* was removed from rocks we observed increases in cover of juvenile canopy-forming species, relative to the control. Therefore, it seems likely that for temporal scales longer than eighteen months, effective removals of *H. rubra* may have a marked effect on the cover of overstorey algae. Thus, abalone activities appear to have a major influence on smaller or juvenile algae but not adult plants.

Effect of regime shift on local populations of abalone

Adult *H. rubra* actively preferred areas of rock covered wholly in NERA and NCA. It seems clear that adult *H. rubra* help to facilitate and maintain NERA and NCA, and the positive association between abalone and NERA and NCA is likely to reflect a mutualisitc relationship. The advantages to the animal include provision of morphogenic cues for larval settlement on the surface of ERA (Morse & Morse 1986, Daume et al. 1999), sources of nutrition and camouflage pigmentation for juveniles (Shepherd & Turner 1985). The direct benefits of NERA and NCA for adult abalone could also include that NERA and NCA are thin, tightly adherent crusts with smooth surfaces that minimize the risk of abalone being dislodged in turbulence (Steneck 1982) or by predators (Shepherd 1975, Shepherd & Turner 1985) and that abalone may also gain increased access to food by sitting on areas covered in NERA and NCA (Steneck 1982, Littler & Littler 1995). Our results suggest that adult *H. rubra* benefits NERA and NCA by removing filamentous and foliose algae, and sediment and sessile invertebrates that can overgrow and shade or smother the underlying NERA and NCA.

Simulated heavy fishing of *H. rubra* can lead to a shift in understorey community structure to a habitat type that is less favourable for adult abalone. The majority of transplanted adult *H. rubra* immediately moved away from NERA and NCA that was overgrown by filamentous and foliose algae, sessile invertebrates and accumulated sediment but not from rocks supporting NERA and NCA. These changes in adult *H. rubra* behaviour are potentially linked to the changes in the surface properties of rocks that prevent or limit abalone attachment, which might result in increased physical stresses and/or risk of predation (Shepherd 1975, Shepherd & Turner 1985).

This shift in algal community structure away from NERA and NCA to habitat covered in filamentous and foliose algae, sediment and sessile invertebrates could have wider ramifications by impacting on *H. rubra* recruitment processes. In California, mass mortalities of the black abalone, *Haliotis cracheroidii* were followed by declines in the cover of NERA and NCA in crevices and increases in the cover of filamentous and foliose algae and sessile invertebrates which in turn led to declines in the density of *H. cracheroidii* recruits and juveniles (Miner et al. 2007). Similarly, declines in the cover of NERA and NCA could potentially lead to reduced availability of morphogenic cues required for *H. rubra* larvae to settle (Daume et al. 1999), reduced availability of food for newly settled abalone (benthic microflora and diatoms, NERA and NCA) and reduced availability of pigment that

affords camouflage protection to juvenile *H. rubra* from predators or prevent or limit juvenile attachment (Shepherd & Turner 1985). We suggest this habitat shift could lead to declines in the density of *H. rubra* recruits and juveniles with eventual flow on effects to adult abundances.

Ecosystems effects of fishing abalone

Simulated intensive harvesting of *H. rubra* on the east coast of Tasmania triggered a shift to an alternative understorey configuration. Both community states arise through positive feedbacks depending on the abundance of abalone. NERA and NCA, resistant to *H. rubra* activities, flourishes in the presence of high densities of abalone, and is preferred habitat for abalone, here the positive feedback loop is that abalone begets NERA and NCA begets abalone. Alternatively a benthos dominated by foliose and filamentous algae, sessile invertebrates and the sediment matrix supports a different positive feedback, in that as the as the abundance of these elements increases, the habitat becomes less preferred by abalone, removing an important mechanism that can reduce cover of filamentous and foliose algae, sessile invertebrates and the sediment matrix.

Understanding the potential for and the dynamics of this shift between alternative benthic states is important in developing fisheries management strategies (Collie et al. 2004, Scheffer & Carpenter 2003, de Young et al. 2008). If the shift to a high cover of sessile invertebrates, foliose algae and the sediment matrix is continuous, then the extent of recovery of NERA and NCA should be concomitant with the extent of the reduction of abalone fishing. Alternatively, if the shift is discontinuous or catastrophic, resulting in hysteresis, even after the cessation of abalone fishing, the system may take considerable time to recover. This raises the question, once NERA and NCA becomes overgrown, how and whether abalone might overcome habitat covered in filamentous and foliose algae, sessile invertebrates, and partially consolidated sediment matrix to force it to the configuration dominated by NERA and NCA. Our results suggests the possibility that intensive fishing of *H. rubra* could result in a discontinuous phase shift given the relationship between abalone the benthic state of filamentous and foliose algae, sessile invertebrates and sediment matrix, is self-reinforcing in the context of its effect on abalone behaviour and local abundances and potential impacts on recruitment processes.

Conclusions

In the past decade, many scientists have recognized the links between fisheries and regime shifts (Tegner & Dayton 2000, Jackson et al. 2001, Scheffer et al. 2001, Myers & Worm 2003, Scheffer & Carpenter 2003, Ward & Myers 2005, Dakalov et al. 2007, de Young et al. 2008). Field data are being explored with more powerful techniques, and models are being used to address implications of important aspects such as, environmental fluctuations and spatial complexity (Scheffer & Carpenter 2003, Schroder et al. 2005, Mumby et al. 2007). Our results demonstrate that small-scale experimental manipulations can also play an important role in illuminating the mechanisms of regime shift and the nature of strong feedbacks, which maintain the persistence of alternative stable states. These results can be used develop management strategies to prevent regime shifts, to reveal how common and under what conditions alternative states may occur, and to guide strategies for future research and the restoration of preferred configurations of marine ecosystems (Hughes et al. 2005, Beisner et al. 2003, Carpenter et al. 2008, de Young et al. 2008).

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CHAPTER 7: ECOLOGICAL INTERACTION BETWEEN ABALONE AND OTHER SPECIES AND BENTHIC HABITAT: IMPLICATIONS FOR ECOSYSTEMS BASED MANAGEMENT

ABSTRACT

Ecosystem based management (EBM) is an integrated approach that considers the interactions between species and other components of the system. Here we review research on the ecological interactions between commercial *Haliotis* spp., and other components of temperate rocky reef ecosystems, and their implications for EBM. There are important ecological interactions between abalone and urchins, rock lobsters and the benthic community, however the nature of these interactions differs considerably between life stages and ecosystems. In Australia and California, adult and juvenile abalone grazing has an important influence on benthic community structure. In Canada, California, Japan and South Africa, there are positive interactions between adult urchins and juvenile abalone, because abalone gain increased access to food and reduced risk of predation by sheltering beneath the spine canopy of urchins. In contrast, in Australasia and California, urchins negatively impact on adult abalone, behaviour, movement, growth and survivorship. In Australasia, California, Canada and South Africa there are complex interactions between predators, urchins and abalone. The challenge for EBM is to manage the abundances of predators and grazers in the system to prevent regime shifts from productive and diverse algal beds to barrens or benthos covered in filamentous and foliose algae, sessile invertebrates and accumulated sediment, which then become unsuitable for abalone populations.

INTRODUCTION

Globally, many commercial fisheries species are in decline (Jackson et al. 2001, Pauly et al. 2002, Myers & Worm 2003, Scheffer & Carpenter 2005). Major anthropogenic stressors include global climate change (Walther et al. 2002), invasive species (Carlton & Geller 1993), fishing (Jackson et al. 2001, Myers & Worm 2003), pollution, nutrients, (Islam & Tanaka 2003), and habitat loss (Lotze et al. 2006). These stressors can result in declines in species abundances, and alter the ecological interactions between species, and their environment (Scheffer & Carpenter 2003, Folke et al. 2004, Hughes et al. 2005). With the increasing risk of multiple anthropogenic stresses there is an unprecedented risk of a dramatic shift in species composition, known as catastrophic, phase or regime shifts, which are often long lasting and difficult to reverse (Scheffer & Carpenter 2003, Folke et al. 2004, Hughes et al. 2005). Hence, scientists and managers have an urgent need to understand the ecological interactions between species and their environment that support or undermine the ecosystems resilience to human impacts (Mangel & Levin 2005, Levin & Lubchenco 2008).

Abalone are herbivorous macro-invertebrates, that are primarily located in the intertidal and subtidal areas of temperate rocky reef ecosystems (Shepherd 1973a, Shepherd et al. 2001, Jenkins 2004). Abalone fisheries have traditionally focused on single-species based management strategies (Shepherd et al. 2001, Jenkins 2004). However, with growing awareness that abalone both affect and depend on the dynamics of the rocky reef ecosystems that support them, there is impetus to develop and apply ecosystem based management (EBM) strategies to abalone fisheries to complement the established practises based on single species (Jenkins 2004, Shepherd et al. 2001). This approach requires a good understanding of the interactions between abalone and other components of the temperate rocky reef ecosystem to manage the systems resilience to human impacts (Mangel & Levin 2005, Levin & Lubchenco 2008). Here we review research on the impacts, strength and direction of direct and indirect interactions between abalone and other species and their environment (benthic habitat, competitors, commensualists, pathogens, predators and complex interactions), focusing particularly on juvenile and adult life stages. We compare and contrast these interactions worldwide and consider their implications for EBM strategies for diverse *Haliotis* spp. fisheries.

Interactions between abalone and benthic habitat

Assessing the role of abalone in structuring algal communities on temperate rocky reefs is crucial for developing and applying EBM strategies (Schiebling 1994, Kitting 1997, Jenkins 2004). Recent research suggests *Haliotis* spp. grazing can have important small-scale influence on benthic community structure (Kitting 1997, Chapter 6). Experimental removals of adult *Haliotis rubra* from rocks in marine protected areas in Tasmania, Australia, resulted in smothering and/or overgrowth of encrusting red algae (ERA) by sediment, filamentous and foliose algae and sessile invertebrates (Chapter 6). Similar results have also been obtained following removals of adult *H. rubra* in Victoria (Hammer pers. comm.) and juvenile *Haliotis rufescens* in California (Kitting 1997). In contrast, experimental removals of adult *Haliotis roei* from plots in Western Australia, led to only small and non-significant changes in the intertidal benthic community (Scheibling 1994). Further study is required to determine the generality of these results to other species. However, in Australia and California, EBM must focus on maintaining sufficient densities *Haliotis* spp. to maintain understorey community dominated by ERA.

EBM needs to consider feedbacks in interaction topologies that involve abalone, and this is particularly important in the case of positive feedbacks given their potential to be stabilising with respect to one particular dynamic or community configuration but destabilising to another (Scheffer et al. 2001, Collie et al. 2004). Recent surveys in Australia, have demonstrated a positive association between the cover of ERA and the abundance of abalone across several depths and locations (Valentine et al. unpublished manuscript, Chapter 5). ERA provides an important settlement cue for abalone larvae (Morse & Morse 1984, Daume et al. 1999), and shell pigmentation associated with feeding also aids camouflaging juveniles from predators (Shepherd & Turner 1985). In addition, the benthic microflora and diatoms that grow on these algae are part of the early diet of juvenile abalone (Shepherd 1973a, Shepherd & Turner 1985). Adult *H. rubra* actively preferred areas of rock covered in ERA (Chapter 6). Because adult abalone activity can be important in maintaining ERA (Chapter 6), the interaction between abalone and ERA is characterised as a positive feedback loop; ERA resistant to abalone grazing flourish in the presence of high densities of abalone, reinforcing ideal habitat for abalone.

Intensive fishing of abalone can result in a shift to an alternative stable benthic community which then becomes unsuitable for abalone (Chapter 6).

This establishes a positive feedback loop which may have important implications for the long-term persistence of abalone population. In Australia, the majority of transplanted adult *H. rubra* immediately moved away from ERA that was overgrown by filamentous and foliose algae, sessile invertebrates and accumulated sediment but not from rocks supporting ERA (Chapter 6). Thus, simulated heavy fishing resulted in a different positive feedback to the detriment of abalone, because abalone removal induced a shift in benthic community structure that was much less preferred by both juvenile and adult abalone (Chapter 6). Recruitment failure of black abalone in California has also been linked to a shift in habitat from ERA to sessile invertebrates, filamentous and foliose algae, following mass-mortality of black abalone populations (Miner et al. 2006). These results suggests the possibility that intensive fishing of abalone could result in a discontinuous phase shift given the relationship between abalone the benthic state of filamentous and foliose algae, sessile invertebrates and sediment matrix, is self-reinforcing in the context of its effect on abalone behaviour and local abundances recruitment processes (Miner et al. 2006, Chapter 6). Clearly, where depletion of abalone causes a shift in benthic habitat that is less suitable for abalone, it is important that EBM considers these dynamics.

Interactions between abalone urchins and benthic habitat

There are a range of potential abalone commensalists, and competitors including chitons, limpets, topshells, other gastropods (Laws 1970, Scheibling et al. 1990, Hideki et al. 2001, Stotz et al. 2006), sea stars (Blanchette et al. 2005) and urchins (Lowry & Pearce 1973, Shepherd 1973a). However there has been little or no research into the direction and effects of interactions between abalone and most of these groups, with the exception of urchins (Deacon 1973, Shepherd 1973b, Tegner & Levin 1982, Andrew & Underwood 1992, Andrew et al. 1998, Kapov et al. 1999, Strain & Johnson 2009, Chapter 2, 3 and 4). The nature and effects of interactions between abalone and urchin differs substantially between ecosystems (Shepherd 1973b, Tegner & Levin 1982, Andrew et al. 1998, Naylor & Gerring 2001, Strain & Johnson 2009).

In southeast Australia (Shepherd 1973b, Andrew & Underwood 1992, Andrew et al. 1998, Johnson et al. 2005), New Zealand (Naylor & Gerring 2001), and California (Lowry & Pearce 1973, Tegner & Levin 1982, Karpov et al. 1998), adult abalone and urchins share a similar dietary spectrum and habitat, and it has been widely speculated that these 2 herbivores compete for

algal resources. Experimental introductions of urchins (*Centrostephanus rodgersii*) to plots in intact algal beds in Australia and New Zealand (*Evechinus chloroticus*) resulted in both juvenile and adult abalone dispersing (Naylor & Gerring 2001) and seeking shelter in cryptic hiding (Chapter 2). In enclosures with added *C. rodgersii,* adult *H. rubra* showed reduced growth, reproduction and survival relative to enclosures without urchins within 6 months of initiating the experiment (Strain & Johnson 2009 Chapter 3). There were no similar effects of abalone on urchins (Chapter 2, 3) and so, in this sense, the interaction is asymmetrical. Similarly in California, inclusion of adult *Strongylocentotus franciscanus* in tanks had a negative effect on the total weight of adult *Haliotis rufescens* relative to tanks without urchins (Tegner & Levin 1982). These results suggest urchins can negatively impact on abalone accessibility and productivity for fisheries. In these systems, EBM is likely to be focused on reducing urchin numbers (Shepherd 1973b, Lowry & Pearce 1975, Tegner & Levin 1982, Andrew & Underwood 1992, Andrew et al. 1998, Naylor & Gerring 2001, Johnson et al. 2005, Strain & Johnson 2009, Chapter 2, 3).

Urchin grazing can have a major influence on the structure and function of temperate rocky reef ecosystems (for review:Lawrence 1975, Breen & Mann 1976, Tegner & Dayton 2000). Studies in Australasia (Fletcher 1987, Johnson et al. 2005, Ling 2008), the North Atlantic (Chapman and Johnson 1990, Elnerand & Vadas 1990), North Pacific (Dayton 1975) and in South America (Santelices & Ojeda 1984) have demonstrated that urchin grazing can results in a catastrophic shift from productive and diverse algal beds to an alternative stable barrens habitat devoid of foliose and filamentous algae and dominated by the urchin (Steneck et al. 2001, Steneck 2003). In southeast Australia, urchin grazing poses a major threat to kelp beds and the commercial fisheries they support (Andrew & Underwood 1992, Andrew et al. 1998, Johnson et al. 2005, Chapter 4). Juvenile and adult abalone only recolonised barrens after the urchin was removed and algal regrowth allowed to develop (Andrew et al. 1998, Chapter 4). These results suggest that lack of food and loss of canopy algae explains the low densities of some *Haliotis* spp. on urchin barrens (Andrew et al. 1998, Edgar et al. 2004, Chapter 4). These results are consistent with surveys at much larger scales which demonstrate that abalone are found at much lower densities on barrens habitat than on adjacent reef supporting seaweed cover (Andrew & Underwood 1992, Andrew et al. 1998, Karpov et al. 1998, Johnson et al. 2005). Thus, Australasia, and by extension to other regions where urchins barrens can develop in regions supporting abalone fisheries, EBM must

focus on reducing the abundances of urchins and associated barrens habitat to optimise the abalone fishery.

Interactions between abalone and urchins are not necessarily negative. In Canada (Tomascik & Holmes 2003), California (Tegner & Dayton 1981), Japan (Kojima 1981) and South Africa (Tarr et al. 1996, Day & Branch 2000), densities of some species of urchin and abalone are positively correlated because juvenile abalone benefit from sheltering beneath the spine canopy of adult urchins. Advantages to the juvenile abalone include increased access to drift kelp and reduced risk of predation (Day & Branch 2002 a, b, Rodgers-Bennett & Pearse 2001). This positive interaction between urchins and juvenile abalone is clearly an important consideration in EBM. Experimental removals of *Parechinus angulosus* from plots in South Africa resulted in significant declines in the abundance of *Haliotis midae* recruits and juveniles (Day & Branch 2002a). Research in California also demonstrated that there were much higher abundances of juvenile *H. rufescens* and *H. walallensis* on protected reefs where there were high abundances of urchins, as opposed to areas and urchins were experimental removed (Rodgers-Bennett & Pearse 2001). In areas such as California and South Africa where the spine canopies of urchins enhance abalone recruitment, it is important to increase the abundances of urchins but not to a point where there is significant risk of urchins overgrazing intact algal beds.

Urchin grazing could also have a positive impact on abundances of juvenile abalone (Andrew & Underwood 1992, Andrew et al. 1998, Day & Branch 2002c, McShane 1991, Chapter 4). In many systems, urchin grazing is important in maintaining habitat covered by ERA and associated diatom and microflora communities (Day & Branch 2000c) and these algae provide important habitat for abalone larvae and juveniles (Morse and Morse 1984, Shepherd & Turner 1985, Daume et al. 1999). However experimental studies in South Africa and Australia have found very little evidence to support this hypothesis (Day & Branch 2002c, Chapter 4). Field experiments in southeast Australia found that there was a much lower density of adult and juvenile *H. rubra* and cover of ERA in small barrens patches from which *C. rodgersii* and all regrowth was removed compared to patches where *C. rodgersii* was removed but regrowth allowed, and in patches in intact algal beds (Chapter 4). In their laboratory study, Day & Branch (2002c) found that there were no detectable effects of *Parenchinus angulosus* grazing on the quantity or composition of the diatoms and microflora community on artificial coralline mimics relative to treatments without urchins. However removal of *P.*

sediment, and declines in the densities of *Haliotis midae* recruits and juveniles (Day & Branch 2002 b, c). This suggests that *p. angulosus* grazing might be important maintaining a low cover of blue green and filamentous microalgae which can trap sediment resulting in negative impacts on juvenile *H. midae,* however this idea requires critical testing (Day & Branch 2002 b, c).

Understanding the positive and negative effects of urchin grazing on abalone is clearly important for EBM. In South Africa and other ecosystems where urchins ostensibly rely heavily on drift algae and do not tend to form barrens, an increase in the density of urchins and associated grazing is likely to have a positive impact on the densities of abalone recruits and juveniles, although the mechanisms and impacts on adult abalone remain unknown (Day & Branch 2002 b, c). In Australasia, North Pacific and South America, where urchins have the propensity to form barrens, urchins at low densities could have a positive impact on the densities of abalone because of their ability to maintain habitat dominated by ERA with intact canopy algae (e.g. Johnson et al. 2005). As the densities of the urchin and intensity of the grazing increases, the canopy algae is eventually consumed which results in negative impacts on densities of abalone (Andrew 1993, Chapter 2, 3, 4, Edgar et al. 2004). In California, the optimal density of urchin is an intermediate level such that they do not dominate all the available resources and form barrens but still allowing sufficient numbers for protection of juvenile *H. rufescens* and *H. walallensis* (Tegner & Levin 1983, Rogers-Bennett et al. 2001).

Impact of pathogens on abalone

A variety of abalone parasites have been identified, including sponges (Shepherd & Breen 1992), annelids (Sinclar 1963, Shepherd 1975a, Kojima & Imajima 1982), molluscs (Blake & Evans 1972), polychaetes (Oakes & Fields 1996, Kuris & Culver 1999), bivalves (Cox 1962), protozoa (Goggin & Lester 1995) and trematodes (Rice et al. 2006). These species either bore into the shell or live in the abalone muscle, gonad or brain tissues. Known impacts of these parasites include declines in abalone growth and reproductive capacity (Kojima & Imajima 1982, Goggin & Lester 1995, Oakes & Fields 1996, Lleonart et al. 2003, Rice et al. 2006). Also, if the abalone shell is weakened by parasites, the animal may become more vulnerable to predators (Shepherd & Breen 1992), and abalone infected with parasites may also be more susceptible to disease (Goggin & Lester 1995).

Numerous bacteria and viruses can infect wild abalone population however only a small number of have been identified (Bower et al. 1994, Bower 2000). Abalone diseases are typically classified arbitrarily into three categories, *viz.* severe diseases which cause mass mortality of wild stock and are therefore of cause for major concern for fisheries (e.g. the virus amyotrophic), diseases of less concern which live in the tissues of the abalone or have special life requirements (e.g. coccidian in the abalone kidney or helmiths) and diseases that are only detrimental under certain environmental conditions (e.g. fungi) (Lafferty & Kuris 1993, Bower 2000). Diseases causing mass mortality in wild abalone populations include the withering syndrome bacterium in California (Lafferty & Kuris 1993), the blister bacterium in France (Handlinger et al. 2001) and, more recently, the viral ganglioneuritis in southeast Australia (Prince 2007).

Abalone parasite load and susceptibility to diseases appears to vary markedly between species, habitats and regions (Shepherd & Breen 1992). The challenge for EBM is to prevent accidental introductions and spread of parasites and diseases in wild abalone (Mo 1994). In some countries, introduced parasites and diseases have had devastating impacts on wild abalone stocks (Mo 1994, Tegner et al. 1996). Development of effective strategies to prevent the introduction of parasites and diseases requires further research into cost effective means of detecting and identifying parasites and diseases, assessing the impacts of new and existing parasitic species and diseases on wild abalone, and developing cost effective quarantine practises (Farley 1992). Strategies to limit the spread of introduced parasites and diseases must focus on regulating the spread of parasites and diseases from aquaculture and translocated abalone (Bower 2000) and isolating currently infected wild stocks. These strategies are likely to be important in preventing mass mortality of abalone populations and in some ecosystems the potential for a catastrophic shift to an alternative and stale benthic reef community (Miner et al. 2006, Chapter 6)

Interactions between abalone and predators

Predators can have a major impact on prey abundance, behaviour and size (Sala et al. 1998). The importance of predator-prey interactions for EBM depends on the impacts of the predator on abalone and the dependence of the predator on abalone as prey (Jenkins 2004). Predators of abalone can be broadly divided into five groups (a) crabs and rock lobsters, (b) fishes, rays

and sharks, (c) gastropods, octopi and other molluscs, (d) mammals (Table 1). Notably, although numerous predators of abalone have been identified, we could only find detailed field studies on 13 species.

Crabs and rock lobsters

Large crustaceans are among the best known abalone predators (Shepherd & Clarkson 2001). Crabs and rock lobsters have significant impacts on the abundance, behaviour and size of juvenile abalone (Shepherd & Breen 1992). Caging studies have estimated have the crabs *Paguristes frontalis* (Mower & Shepherd 1988, Shepherd 1990) and rock lobster *J. edwardsii* (Pederson et al. unpublished data) in southeast Australia and the crabs *Loxorhynchus grandis, Taliepus nuttallii, Cancer antennarius, Paguristes chabrus, Neciocarcinus tuberculosus* in California (Tegner & Butler 1989) can consume 15-20% y^{-1} of the juvenile abalone population at a given site. Juvenile abalone spend more time in cryptic shelter to avoid these predators (Shepherd 1973a, Pederson et al. unpublished data), which is likely to negatively impact their feeding and growth (Momma 1980), although this idea requires further testing.

Despite widespread recognition of crustacean predation on abalone, the importance to crustaceans of abalone as prey is not well researched. Studies in southeast Australia based on DNA analysis of lobster faecal pellets suggest that *H. rubra* is an important dietary component of *J. edwardsii,* even during periods of low catchability (Redd et al. unpublished data). Collectively these observations indicate that interactions between crustaceans and juvenile abalone are an important consideration for EBM, but further work is required to properly quantify the effects on abalone populations and assess whether the magnitude of effects is similar across all ecosystems supporting abalone.

Fishes, rays and sharks

Fishes and elamobranchs are the most diverse and abundant guild of abalone predators. In southeast Australia, Shepherd (1990) estimated from shell collections that rays (*D. brevicaudata* and *M. australis*) can consume 70 to 90% y^{-1} of juvenile and adult *H. laevigata* populations while the impacts of fishes were not as severe. A decade later, Shepherd & Clarkson (2001) estimated that *N. tetricus* can eat 38% y^{-1} of juvenile *H. laevigata* and *H. scalaris*. The limited research to date suggests that despite the impact of these predators, abalone do not form an important component of their diet

(Shepherd & Clarkson 2001, Morton et al. 2008). Data are still too few to assess whether interactions between abalone and fishes, rays and particularly sharks are important in the context of EBM.

Gastropods and other molluscs

Numerous species of molluscs have been reported as predators of both juvenile and adult abalone (Ambrose 1983, Tegner & Butler 1985, Shepherd 1990, Kojima 1992), but most authors do not suggest that these predators are important sources of abalone mortality (Shepherd & Breen 1992). One notable exception in California, Japan, the Mediterranean and South Africa, is *O. vulgaris* (Ambrose 1983, Tegner & Butler 1985, Kojima 1992, Smith 2003). Estimates from shell midden collections suggest that *O. vulgaris* can consume 12-20% y^{-1} of the juvenile abalone population at a site (Ambrose 1983, Tegner & Butler 1985, Kojima 1992). Moreover, stomach content analyses demonstrated that juvenile abalone are an important component (15-25 % by volume) of *O. vulgaris*' diet (Ambrose 1983, Smith 2003). However, both these methods are likely to overestimate the importance of this interaction because abalone shells remain in octopus stomachs and at midden sites longer than soft bodied prey.

Mammals

Sea otters are a major predator of abalone in some areas of the northeast Pacific rim (Estes & Palminsanso 1974, Estes et al. 2003), where they can inflict instantaneous mortality rates of 0.3-1.0 y^{-1} (Lowry & Pearse 1973, Breen et al. 1982, Hines & Pearse 1982). Sea otters consume both juvenile and adult abalone. Abalone populations outside of the range of sea otters typically grow to a larger size and individuals spend less time in cryptic habitat (Lowry & Pearse 1973, Hines & Pearse 1982). The impact of this behavioural response on abalone growth has not been studied. The dietary importance of abalone to sea otters varies between regions and through time (Limbaugh 1961). Studies in California have suggested that urchins are the most important prey of otters but abalone become more important as the abundances of urchins decline (Estes et al. 2003). Sea otters have been hunted to extinction in many regions and their importance in EBM management is dependent on population recovery or reintroduction in specific areas (Breen et al. 1982).

Sea stars

Some sea stars are able to prey on and scavenge juvenile and adult abalone (Shepherd & Breen 1992), but abalone have a well developed escape response to sea stars and so sea stars do not appear to inflict significant mortality (Shepherd & Breen 1992, Jenkins 2004). However, there may be exceptions to this generalisation. McShane & Smith (1986) recorded high mortality of juvenile *H. rubra* in Victoria, Australia, at sites where the sea star *C. muricata* was abundant, and Tegner & Butler (1989) give evidence of significant predation by *p. helianthoides* and *A. sertlifera* on juvenile *H. rufescens* in southern California. However, neither of these studies presents data on predation rates or the importance of abalone in the diet of these species.

Table 1. Summary of field studies examining interactions between predator and abalone, at different life stages and in different regions.

Study	Predator	Abalone	Region	Life stage	Method
McShane & Smith (1986)	*Coscinasterias muricata*	*H. rubra*	Australia	Juvenile	Surveys, experiments
Tegner & Butler (1985, 1989)	*Pycnopodia helianthoides, Astrometris sertlifera*	*H. rufescens*	USA	Juvenile, Adult	Surveys, experiments
Ambros (1983)	*O. vulgaris*	*Haliotis tuberculata*	Mediterranean	Juvenile, Adult	Stomach contents, shell collections
Kojima (1992)	*O. vulgaris*	*H. discus discus*	Japan	Juvenile, Adult	Shell collections
Tegner & Bulter (1985, 1989)	*O. vulgaris*	*H. rufescens*	USA	Juvenile, Adults	Shell collections
Smith (2003)	*O. vulgaris*	*H. midae*	South Africa	Juvenile, Adults	Stomach contents, shell collections
Shepherd (1990)	*Dasuatis brevicaudata, Myliobastis austrlis*	*H. laevigata*	Australia	Juvenile	Surveys, shell collections
Pederson et al. (2008)	*Jasus edwardsii*	*H. rubra*	Australia	Juvenile, Adult	Surveys, experiment
Tegner & Butler (1989)	*Loxorhynchus, Taliepus, Cancer, Paguristes*	*H. rufescens*	USA	Juvenile	Surveys
Mower & Shepherd (1988)	Crustacea	*H. laevigata, H. scalaris*	Australia	Juvenile	Surveys, experiments
Shepherd (1990)	Crustacea	*H. laevigata*	Australia	Juvenile	Shell collections,

					surveys
Shepherd & Clarkson (2001)	*Notolabrus tetricus*	*H. laevigata, H. scalaris*	Australia	Juvenile	Surveys, experiments, stomach contents
Breen et al. (1982)	*Enhydra lutris*	*H. kamtschatkana*	Canada	Juvenile, Adults	Surveys
Estes & Palmisano (1974) Estes et al. (2003)	*E. lutris*	*H. rufescens*	USA	Juvenile, Adults	Surveys, experiments, stomach contents
Hines & Pearse (1982)	*E. lutris*	*H. rufescens, H. walalensis, H. kamtschatkana*	USA	Juvenile, Adults	Surveys
Lowry & Pearse (1973)	*E. lutris*	*H. rufescens*	USA	Juvenile, Adults	Surveys

Complex interactions between abalone and other species

Understanding the complex interactions between abalone and multiple other species is also important for EBM. Recent studies in South Africa, Australia and California suggest there are complex interactions between abalone, urchins and rock lobsters. Field surveys in South Africa, demonstrated that an increase in the abundance of rock lobsters resulted in a significant decrease in the abundance of urchins and juvenile abalone, which depend on adult urchins for protection from predators and increased access to food (Day & Branch 2000, Mayfield & Branch 2000). In contrast, experimental manipulations in California and Australia have demonstrated rock lobsters are major predators of both abalone and urchins but their preferred prey are urchins (Tegner & Levin 1983, Ling & Johnson unpublished manuscript, Pederson et al. unpublished manuscript). In both these systems, increases in the density of large rock lobsters will lead to a decrease in the density of urchins (Tegner & Levin 1983, Ling & Johnson unpublished manuscript, Pederson et al. unpublished manuscript) and may result in an increase in the densities of adult abalone through release from competition with the urchins (Lowry & Pearse 1973, Karpov et al 2000, Tegner & Dayton 2000, Strain & Johnson 2009, Chapter 2, 3). However in California, a decrease in the densities of urchins could also result in a decrease in the densities of juvenile abalone due to increased predation pressure. Thus, the interactions between abalone, urchins and rock lobster are clearly an important consideration for EBM.

In these systems, the challenge for EBM is to manage the abalone, rock lobster and urchins fisheries to prevent the catastrophic shift to urchin barrens. In South Africa, there is a small fishery for rock lobsters and no urchin or abalone fishery. EBM should focus on maintaining a lower density of rock lobsters and a higher density of urchins to optimise the density of abalone, but not to the point of urchin barrens formation. In Australasia, rock lobster and abalone form the basis of large and valuable fisheries, however the urchin fishery is small (Andrew et al. 1998, Jenkins 2004, Worthington & Blount 2003). EBM must decrease the fishing pressure on large rock lobsters, and increase the fishing pressure on urchins to prevent the shift to barrens. In California, EBM must maintain an intermediate density of rock lobsters and urchins to prevent the shift to barrens but still allowing sufficient numbers for protection of juvenile abalone (Tegner & Levin 1983, Rogers-Bennett et al. 2001).

Implications for EBM

There is renewed interest in the nature, effects and strength of interactions between abalone and other species and their environment in the context of EBM. We demonstrated in Australasia, California, Japan, and South Africa, there are important interactions between abalone, urchins and rock lobsters, and the benthic community. In these systems, urchin grazing can have a major influence on the structure and function of the productive and diverse algal beds (Lawrence 1975, Breen & Mann 1976, Tegner & Dayton 2000, Ling 2009, Chapter 4). In Australia and California, abalone grazing can also be important in structuring the benthic community Kitting et al. 1997, Miner et al. 2006, Chapter 6). Intensive fishing of urchin predators and/or abalone is a major anthropogenic stressor that can result in a catastrophic shift between alternative and stable reef states with the potential for a strong hysteresis effect (Andrew & Underwood 1992, Kiting et al. 1997, Andrew et al. 1998, Steneck et al. 2003, Johnson et al. 2005, Miner et al. 2006, Ling 2008, Chapter 4 and 6). These catastrophic shifts in temperate rocky reef ecosystems will negatively impact on local biodiversity and commercial reef based fisheries they support (Chapman & Johnson 1990, Tegner and Dayton 2000, Scheffer & Carpenter 2003, Folke et al. 2004, Hughes et al. 2005, Ling 2008, Chapter 4 and 6).

The challenge for EBM is to manage the densities of grazers and predators to reduce the risk of a shift to urchin barrens and in some systems to benthos covered in filamentous and foliose algae, sessile invertebrates and accumulated sediment (Ling & Johnson unpublished manuscript, Chapter 6). In Australasia and California, EBM must focus on increasing the abundances of large legal sized rock lobsters (carapace length > 140 mm) and abalone (shell length <100 mm), (Ling & Johnson unpublished manuscript). This could be achieved by the introduction of total allowable catch limits or translocations of large legal sized rock lobsters and abalone. In Australasia, EBM should also develop the urchin fisheries (Andrew et al. 1998, Jenkins 2004, Worthington & Blount 2003, Ling 2009). In contrast, in South Africa, EBM must try to increasing the density of legal sized abalone, by developing fisheries for large legal sized rock lobsters (Day & Branch 2000, Mayfield & Branch 2000). Thus, scientists and managers require a robust understanding of the ecological interactions between abalone and other species to support the resilience of temperate rocky reef ecosystems to fishing pressures (Mangel & Levin 2005, Levin & Lubchenco 2008).

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